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Research Document 2006/011 | **Document de recherche 2006/011**

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Effects of Shellfish Aquaculture on Fish Habitat

Effets de la Conchyliculture sur l'Habitat du Poisson

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This document is available on the Internet at: Ce document est disponible sur l'Internet à:
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ISSN 1499-3848 (Printed / Imprimé)
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Canada

2007-00187

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ABSTRACT

The purpose of this document is to provide information about the role of bivalve culture in the ecosystem to enable habitat management to make informed ecosystem-based management decisions with respect to the bivalve culture industry. We do this by considering the roles of bivalves in the ecosystem under natural conditions, describing culture methods and conditions used in Canada and elsewhere, and subsequently evaluating whether these roles are mimicked under aquaculture conditions.

To date, much research (and regulation) has focused on sedimentation processes and their influence on biogeochemical and biological processes in sediments below suspended bivalve culture operations. Similarly, much effort has been directed to developing production carrying capacity models. Such models typically focus on water column (phytoplankton, zooplankton, nutrients and detritus) and benthic (nutrients) processes to ensure that harvests may be maximized.

These approaches are quite well developed and go some distance towards allowing for ecosystem-based management. That being said, they also provide a somewhat truncated and negative view of the role of bivalve culture in the ecosystem. In this document, we develop the model that many ecosystem services provided by bivalve culture are in fact positive and may largely compensate for the more negative effects that are often considered. We concentrate on macrofauna (macroinvertebrates and fishes) and species directly associated with bivalves in culture and suggest that these organisms should be considered more often and formally when decisions are made with respect to bivalve culture operations. We also highlight some issues that we feel need be better addressed so that true ecosystem-based management may be practiced.

A review of the literature shows that bivalves are very important in many ways in the way they interact with the environment. They may exert considerable influence on planktonic communities and nutrient cycling. Through a series of mechanisms, they also greatly promote the diversity and productivity of the assemblages associated with them and may have cascading effects on the ecosystem as a whole.

The main species cultured in eastern Canada are the native mussel (*Mytilus edulis* and *Mytilus trossulus*) and the American oyster (*Crassostrea virginica*). On the West Coast, the main cultivated species are the Pacific oyster (*Crassostrea gigas*) and the manila clam (*Venerupis philippinarum*), both of which are not native to that area. Mussels are mostly farmed in longline systems whereas oysters in eastern Canada are mostly in bottom or off-bottom culture. On the West Coast, oysters are culture both on the bottom and off-bottom as well as increasingly in suspended culture. Spat on the East Coast is almost all form wild set whereas the reverse is true on the West Coast.

On the whole, it was found that bivalves in culture played much of the same roles as do bivalves under natural conditions. That being said, the greater concentration of bivalves in culture does lead to some negative effects on the ecosystem due to increased organic loading in the vicinity of the farms and to harvesting in bottom and off-bottom culture. On the other hand, bivalve culture operations also function more or less as do artificial reefs. In suspended bivalve culture, the abundance of fouling organisms and large mobile species that are associated with these fouling organisms and the abundance of macroinvertebrates

and fishes directly under culture operations was, when evaluated, consistently great. Some work has shown that the presence of these species may compensate for any losses directly below suspended culture operations. Similar increases in associated species have also been observed in off-bottom culture operations. Interactions between bivalve culture and birds and marine mammals are variable.

A number of methods are discussed to address sampling strategies for the suite of organisms that we feel should be included in the evaluation of the influence of bivalve culture in the ecosystem. We also briefly outline issues concerning aquatic invasive species in bivalve culture. We finish up by highlighting certain knowledge gaps and make recommendations for future research.

RÉSUMÉ

Le présent document traite du rôle que jouent les élevages de bivalves dans l'écosystème. Grâce à l'information qu'il contient, les gestionnaires de l'habitat pourront prendre des décisions éclairées sur cette industrie et ce, en tenant compte de l'écosystème. Nous avons ainsi examiné le rôle des bivalves dans les écosystèmes naturels ainsi que les méthodes et les conditions d'élevage observées au Canada et ailleurs. Nous avons ensuite évalué si le rôle joué par ces organismes en milieu naturel était reproduit en milieu conchylicole.

Jusqu'à maintenant, nombre de recherches (et de mesures réglementaires) ont été axées sur la sédimentation ainsi que sur l'effet qu'a ce phénomène sur les processus biogéochimiques et biologiques qui surviennent dans les sédiments en dessous des installations d'élevage de bivalves en suspension. Nombre d'efforts ont aussi été consacrés à l'élaboration de modèles de la capacité biotique pour la production. Ces modèles évaluent habituellement la colonne d'eau (phytoplancton, zooplancton, sels nutritifs et détritus) et les processus benthiques (sels nutritifs) pour optimiser la production.

Ces approches, qui sont assez avancées, tiennent compte jusqu'à un certain point de la gestion écosystémique. Toutefois, elles projettent une image légèrement incomplète et négative du rôle joué par les élevages des bivalves dans l'écosystème. Nous élaborons donc sur le fait que les nombreux rôles joués par les élevages des bivalves dans l'écosystème sont en réalité positifs et peuvent compenser en grande partie les effets plus négatifs qui sont souvent pris en considération. Nous examinons aussi la macrofaune (macro-invertébrés et poissons) et les espèces directement associées à l'élevage des bivalves et proposons que ces organismes soient pris en considération plus souvent et de manière plus officielle dans les décisions prises sur les installations d'élevage des bivalves. Nous insistons également sur quelques enjeux qui, à notre avis, doivent être étudiés plus à fond pour qu'une véritable gestion écosystémique puisse être pratiquée.

Selon un examen de la littérature, les bivalves ont une interaction très importante avec l'environnement et ce, à bien des égards. Ils peuvent avoir une incidence considérable sur les communautés planctoniques et le cycle des sels nutritifs. Par une série de mécanismes, ils ont aussi une incidence considérable sur la diversité et la productivité des assemblages auxquels iis sont associés et peuvent avoir des effets en cascade sur l'écosystème dans son ensemble.

Les espèces principales élevées dans l'est du Canada sont les moules indigènes (*Mytilus edulis* et *Mytilus trossulus*) et l'huître américaine (*Crassostrea virginica*). Sur la côte ouest, les principales espèces élevées sont l'huître creuse du Pacifique (*Crassostrea gigas*) et la palourde japonaise (*Venerupis philippinarum*), deux espèces exotiques. Les moules sont la plupart du temps élevées sur des filières, tandis que les huîtres, dans l'est du Canada, le sont le plus souvent sur le fond ou dans des parcs flottants. Sur la côte ouest, les huîtres sont élevées sur le fond et dans des parcs flottants, mais on assiste aussi à une progression des installations d'élevage en suspension. Finalement, sur la côte est, les naissains sont presque tous sauvages, tandis que sur la côte ouest, c'est l'inverse.

Dans l'ensemble, on a constaté que les bivalves d'élevage jouaient en grande partie les mêmes rôles que les bivalves vivant dans des conditions naturelles. Cela étant dit, la concentration de bivalves plus importante des élevages a certains effets négatifs sur

l'écosystème en raison de l'accroissement de la charge biologique à proximité des installations d'élevage et des récoltes pratiquées sur le fond et dans les parcs flottants. Par contre, les élevages de bivalves fonctionnent plus ou moins comme les récifs artificiels. Dans les élevages de bivalves en suspension, l'abondance des salissures et des grandes espèces mobiles associées à ces salissures ainsi que l'abondance des macro-invertébrés et des poissons directement en dessous des installations d'élevage demeure constamment élevée. Certains travaux démontrent toutefois que la présence de ces espèces peut compenser les pertes survenant directement en dessous des installations d'élevage suspendues. On a également observé des augmentations similaires chez les espèces accompagnatrices à l'emplacement de parcs flottants. Les interactions entre l'élevage des bivalves, les oiseaux et les mammifères marins sont variables.

Enfin, nous examinons aussi un certain nombre de méthodes d'évaluation des stratégies d'échantillonnage appliquées à une série d'organismes qui, à notre avis, devraient être incluses dans l'évaluation de l'incidence de l'élevage des bivalves sur l'écosystème. Nous décrivons aussi brièvement les préoccupations soulevées au sujet des espèces aquatiques envahissantes dans l'élevage des bivalves, puis nous terminons en soulignant certaines lacunes dans les connaissances et en formulant des recommandations pour des recherches futures.

1. INTRODUCTION

Many bivalves have a major effect on their environment either directly or indirectly and are thus important ecosystem engineers or foundation species (Gutiérrez et al. 2003; Newell 2004; Ruesink et al. 2005). All the species commonly farmed in Canada and elsewhere fall into this category. Thus, aquaculture of these species may have a considerable effect on the surrounding ecosystems. Although some of the ecological goods and services provided by bivalves in culture may be desirable, others are potentially undesirable. The purpose of this paper is to provide advice for DFO's Habitat Management in reviewing shellfish aquaculture site applications and in assessing ongoing aquaculture operations in the marine environment. This will be done by addressing the following questions:

1) What are the ecological roles of bivalves in natural ecosystems?
2) Are these roles reproduced under aquaculture conditions?
3) What are the effects of this practice on fish habitats?
4) What are the effects of the physical structures used in shellfish aquaculture on fish habitat (including lines, socks, bags, predator control devices, etc.)?
5) How do these effects vary among species, culture techniques, and regionally?
6) How can these effects be assessed or measured?
7) What baseline conditions should be measured to distinguish between the impacts of shellfish culture and background noise and how should these baseline conditions be taken into consideration in assessing and measuring shellfish aquaculture effects on fish habitat in different areas?

In part because of the complex life cycle of bivalves but also because of the diversity of seed sources and environmental conditions, the number and diversity of potential steps in the culture of the different species in the different areas that may have an influence on fish habitats is great (see Table 1). Covering each of these in turn for all the different species being cultured in Canada is beyond the scope of this work. Instead, we will concentrate this review/advice paper on the grow-out step and others that are considered to be nationally or regionally important.

Ideally, scientific advice should be able to provide clear measures for assessing the importance of bivalve culture activities to the surrounding ecosystem and for developing monitoring methodologies. Many scientists and agencies have and will continue to advocate the use of easily measured indices to this end, including geochemical and benthic infaunal indices - information that is easily obtained using remote methods such as benthic grabs. Unfortunately, as we develop further in this paper, these methods ignore other diverse components of the ecosystem - components that often show net "positive" effects to the installation of bivalve culture sites. These effects include the enhancement of the abundance and diversity of many large organisms, including commercial species and prey for commercial species. These positive effects are rarely considered and cannot be captured by using simple geochemical and infaunal measurements of the benthic environment. Furthermore, these effects often directly concern the species that are of the most interest to both managers and the general public. Positive effects on the environment

must be incorporated into "ecosystem-based management" to ensure a holistic view of the role of bivalve culture in the environment. In Canada, the *Fisheries Act* prohibits the "harmful alteration, disruption or destruction" of fish habitat and is administered in accordance with the guiding principle of "no net loss" of the productive capacity of fish habitat (Fisheries and Oceans Canada 1998). This essentially equates to maintaining productive capacity (Minns 1997). How this aspect is measured in the context of aquaculture assessments is rather ambiguous and may rely as much on professional judgment as on fact. The simple geochemical and infaunal measures of benthic impacts often touted as the best measures for monitoring do not address these aspects and other components of the ecosystem must also be considered if true ecosystem-based management is to be applied. To date, most research on bivalve culture-environment interactions has been focused on determining the "production carrying capacity" (*sensu* Inglis et al. 2000) of a given water body. That is, the stocking density of bivalves at which harvests are maximised. We believe that more effort should be spent in determining the "ecological carrying capacity" of the system (*sensu* Inglis et al. 2000), the stocking or farm density which causes unacceptable ecological impacts. That Canada's *Fisheries Act* is applied to ensure that the productive capacity of a system must be maintained is a good basis to work from. Thus, we will address issues about bivalve culture as they relate to the productivity of the ecosystem. Below, we present data from the published literature to develop a more holistic view of the role of bivalve aquaculture in the marine environment and make suggestions for monitoring components of the environment that are not covered under normal benthic sampling and monitoring.

Table 1. Steps in bivalve aquaculture and their potential to influence ecosystem processes (modified from ICES 2005)

1. Seed collection
    a. dredging
        i. disturbance of benthic communities, especially the removal of long-living species
        ii. removal of juveniles from wild populations of target species
        iii. collection of non-target species
        iv. suspension of sediments
        v. release of H_2S and reduction of dissolved oxygen in the water due to oxygen-consuming substances, release of nutrients
    b. artificial collectors
        i. removal of juveniles from wild population of target species
        ii. increasing target and no-target species recruitment succes
        iii. alteration of the hydrodynamic regime
        iv. acting as fish attraction device (FAD)
        v. risk of entanglement for large vertebrates (e.g. marine mammals, sea birds).
    c. hatcheries
        i. chemical pollution (e.g. pharmaceuticals)
        ii. genetic selection
        iii. spread of diseases

d. importation
    i. introduction of alien species
    ii. genetic pollution
    iii. spread of diseases

2. Growout
    a. effects common to all techniques
        i. organic enrichment of seafloor
        ii. providing reef-like structures
        iii. alteration of hydrodynamic regime (current speed, turbulence)
        iv. food web effects: competition with other filter feeders, increasing recycling speed of nutrients, removal of eggs and larvae of fish and benthic organisms
        v. spawning: release of mussel larvae
        vi. providing food for predators of shellfish
        vii. control of predators and pests
    b. bottom
        i. activities to prepare the culture plots, e.g. dredging for predator removal
        ii. removal of associated organisms by dredging and relaying
        iii. competition for space with wild benthos organisms
    c. artificial structures (trestles, poles, rafts, longlines)
        i. acting as artificial reef or FAD (attraction/displacement or enhancement of animals)
        ii. risk of entanglement for large vertebrates (e.g. marine mammals, sea birds).

3. Harvesting
    a. effects common to all techniques
        i. removal of biomass, nutrients
        ii. removal of non-target species
        iii. competition with predators
        iv. scheduling (temporal)
    b. dredging
        i. disturbance of benthos communities, especially removal of long-living species
        ii. suspension of sediments
        iii. release of H2S and decrease of dissolved oxygen in the water due to oxygen-consuming substances, release of nutrients
    c. collection of off-bottom structures

4. Processing
    a. dumping of by-catch
    b. relaying near auction houses
    c. depurating
    d. dumping of shells
    e. effluents from processing plant

2. ROLE OF BIVALVES IN NATURAL ECOSYSTEMS

2.1. Bivalve diversity and life history

The class Bivalvia is part of the phylum Mollusca (chitons, snails, squid, etc.) and comprises about 7500 species (Gosling 2003). As a group, the bivalves are characterized by being laterally compressed, bilaterally symmetrical, and have paired mantle lobes that secrete a calcareous external bivalved shell which is joined at the top by a ligament and protects the body of the animal (Beesley et al. 1998). Over evolutionary time, the gills that underlie the mantle have typically taken over the role of capturing food, filtering it out of the water column by ciliary action. From this basic body plan there have evolved four basic modes of life: being buried in unconsolidated sediments (such as soft-shell and manila clams), cemented onto hard substrates (oysters), attached to the substrate by byssal threads (mussels), and free-living on the bottom (such as scallops). Bivalves are often gregarious and form dense reefs or beds of filter feeding organisms, thus also having a considerable influence on the surrounding ecosystem (Dame 1996). These include all of the species currently cultured in Canada for aquaculture purposes.

Although there is an extreme diversity of life histories in bivalves as a group, all the species that are of commercial importance have a similar life cycle. Briefly, sexes may be separate, combined or variably alternating, depending on the bivalve in question. Spawning usually takes place following some environmental trigger (temperature, light, phytoplankton bloom, etc.) and may occur more than once annually, as Seed (1976) has suggested to occur for *Mytilus edulis*. Fertilization is external and larval development and differentiation occur in the water column. Larvae are typically more or less planktotrophic (feeding in the water column) and may be dispersed over great distances during a typical larval life of 3-5 weeks (Gosling 2003). Settlement and metamorphosis typically occur when larvae have a shell length of 250-300 µm. Settlement is often selective (i.e., on suitable substrates, often filamentous algae or other organisms or else conspecifics) and, with the exception of oysters, is often reversible. Secondary dispersal may also occur, as has been shown for mussels (Bayne 1964; Seed and Suchanek 1992; Lasiak and Barnard 1995), clams (De Montaudouin 1997; Hunt 2004), and scallops (Beaumont and Barnes 1992; Garcia et al. 2003). Thereafter, the growing bivalves are more or less sedentary and typically remain where they settle, baring disturbance events that may displace them over moderate distances.

2.2 Ecological function

A given habitat is often defined by the presence of a single physically dominant species. Hence, mangrove forests, eelgrass beds, oyster reefs, or mussel beds. The species that characterize these habitats usually form large aggregations that are perpetuated through clonal propagation or gregarious settlement (Bruno and Bertness 2001). Most gregarious bivalves have a major influence on the habitat in which they live by altering local physical and biological processes. Such bivalves have variably been termed as foundation species (Dayton 1972; Bruno and Bertness 2001; Bruno et al. 2003) or engineering species (Crooks and Khim 1999; Gutiérrez et al. 2003; Ruesink et al. 2005) because of the way they modify environmental conditions, resource availability, and species interactions. Here, we will use the term "foundation species" as described by Bruno and Bertness (2001) as it infers the

species is relatively large, dominant in terms of biomass or abundance, and has a positive effect on community inhabitants via its presence and not its actions. The term "ecosystem engineers" (sensu Jones et al. 1994, 1997) includes predators and herbivores that, through their actions, have inordinate influence on the environment, such as beavers in ponds or predatory starfish on mussel beds. In this section, we outline some of the influences bivalves in natural habitats have on the surrounding ecosystem as foundation species. We concentrate on three main processes: their influence on the water column as filter feeders, their influence on sedimentation and nutrient fluxes, and their role as habitat for other species and all that this entails.

2.2a Ecological function (Filtration)

The influence of bivalve filter feeding on the pelagic ecosystem is very well studied and is well reviewed in Dame (1996), Prins et al. (1998), and Newell (2004). In short, dense beds of bivalves have been shown to be able to control and or otherwise moderate various planktonic assemblages in natural systems, with feed-backs between the different levels of the ecosystem. As these are well discussed in a companion paper (Chamberlain et al. 2006), we will only briefly outline the relevant points here.

Through filter feeding, abundant bivalve populations have the potential to influence the plankton community (standing stocks and species composition), primary production, water clarity, nutrient cycling, and food webs (Cloern 1982; Officer et al. 1982; Cohen et al. 1984; Yamamuro and Koike 1993; Dame 1996). Bivalves live in a highly dynamic physical environment with both temporal and spatial variability in the quantity and quality of available food (Prins et al. 1998). Advective processes, resuspension and wave action can all affect temporal and large-scale spatial variability in food (Berg and Newell 1986; Fréchette et al. 1989; Asmus et al. 1990; Prins et al. 1996; Smaal and Haas 1997). Smaller scale spatial variability may be a consequence of the filtration activity of bivalves themselves (Fréchette and Bourget 1985; Wildish and Kristmanson 1997), depending on the degree of resuspension of seston (Smaal and Haas 1997) and advection (Prins et al. 1996) in the system.

The feeding response of bivalves to changes in seston concentration varies considerably among species. Some species, such as the eastern oyster, *Crassostrea virginica*, and the blue mussel, *M. edulis*, maintain relatively high clearance rates even when seston concentrations increase (Newell and Langdon 1996; Hawkins et al. 1998). Phytoplankton cells not required for nutrition, in addition to less nutritious detrital and silt particles, are rejected in pseudofeces. In response to increasing seston concentrations, other species of suspension feeding bivalves, such as cockles, clams, and scallops, mainly regulate their ingestion rates by reducing clearance rates and not so much by rejecting excess particles as pseudofeces (Hawkins et al. 1998; Grizzle et al. 2001). The species of bivalves that can exert the greatest influence on benthic-pelagic coupling are those that maintain high clearance rates and reject large numbers of particles as pseudofeces (Newell 2004).

Phytoplankton effects. Dame (1996) reviews studies that provide strong evidence that natural populations of filter feeding bivalves can exert top-down control on phytoplankton in coastal waters and it is unnecessary to repeat this evidence here. Interestingly, some of the most dramatic examples of top down control occur following the rapid population growth of an exotic species of bivalve (Newell 2004). In San Francisco Bay, California,

for exam le, phytoplankton has been shown to be controlled by non-native bivalves, including *Tapes japonica* and *Musculus senhousia* (Cloern 1982; Officer et al. 1982), and *Potamacorbula* spp. (Carlton et al. 1990). Alpine and Cloern (1992) suggests that a summer phytoplankton biomass maximum disappeared in San Francisco Bay following invasion of the suspension-feeding clam *Potamocorbula amurensis*, presumably because of increased grazing pressure by this newly introduced species.

Because bivalve feeding removes both phytoplankton and inorganic particles from the water column, turbidity is reduced. The resulting increased light penetration to the sediment surface can potentially enhance the production of benthic plants, such as seagrasses, algae, and microphytobenthos (Newell and Koch 2004). An increase in light penetration to the sediment surface may be deleterious if "nuisance species" of macroalgae become established: if growth is profuse, water flow may be restricted and plant decay may cause sediment hypoxia (Peckol and Rivers 1995; Taylor et al. 2001).

In waters with substantial rates of bivalve grazing, larger nanoplankton cells may be preferentially removed in comparison with smaller (<3-pm diameter) picoplankton species that are retained less efficiently on the gill of most bivalve species (Newell 2004). This selective bivalve feeding during warmer months, when picoplankton growth is favoured over that of nanoplankton species by warmer waters and changes in the relative abundance of inorganic and organic nitrogen (Malone 1992; Gobler et al. 2002), reinforces seasonal successional cycles in phytoplankton species composition, leading to the situation where picoplankton become relatively more abundant than larger species in areas with shellfish populations (Prins et al. 1998). Such changes in the composition of the phytoplankton community may affect other filter feeding organisms in the ecosystem.

Although filter-feeding bivalves can serve to improve water quality in eutrophic waters by exerting top-down control on phytoplankton populations, eutrophication may affect bivalve populations by affecting the availability of specific phytoplankton. While increased phytoplankton biomass associated with nutrient enrichment may be beneficial to bivalve suspension-feeders, it is now recognized that anthropogenic inputs of N and P alter the ratio of these inorganic nutrients from the typical Redfield ratio of 16:1 (Cloern 1982; Malone 1992; Conley 1999). The optimal ratio of N:P for algal growth is species-specific, so changes in the N:P ratio alters the competitive interaction between phytoplankton species (Rhee 1978) and nutritious species for bivalves may be outcompeted by less nutritious species (Terry 1982).

Zooplankton effects. Although usually not considered in ecosystem dynamics, wild populations of bivalves have the potential to influence zooplankton communities through a number of mechanisms. Recent research on the potential for a benthos-zooplankton trophic loop suggests that the classic model of bivalve filtering of phytoplankton may be inadequate to describe the trophic effects of bivalves on planktonic ecosystems (Wong and Levinton 2006). Bivalves have been shown to consume a diversity of species of micro- and mesozooplankton through experiments monitoring zooplankton clearance from suspension and through examination of digestive tract contents in both field and laboratory studies. Bivalves shown to consume zooplankton include *M. edulis* (Kreeger and Newell 1996; Davenport et al. 2000; Lehane and Davenport 2002; Wong et al. 2003), *Geukensia demissa* (Kreeger and Newell 1996); *Crassostrea gigas* (Le Gall et al. 1997; Dupuy et al. 1999), *Placopecten magellanicus* (Shumway et al. 1987), *Perna viridis* (Wong et al. 2003),

Aequipecten opercularis (Lehane and Davenport 2002), *Mytilus galloprovincialis* (Jasprica et al. 1997) and *Cerastoderma edule* (Lehane and Davenport 2002). More recently, radiotracer (^{14}C) observations, in combination with microscopic observations, have been used to demonstrate that mussels (*M. edulis* and *P. viridis*) could be predators of mesozooplankton (rotifer *Brachionus plicatilis*) (Wong and Levinton 2006). The potential importance of zooplankton in bivalves' diet is illustrated by Wong and Levinton (2004), who showed that *M. edulis* supplied with both phytoplankton and zooplankton demonstrated the best growth performance (and largest egestion rate and size of faecal pellets) when fed a mixture of phytoplankton and zooplankton.

Concentrations of wild bivalves may have a very high reproductive output. The importance of the addition of this mass of larvae into the receiving ecosystem remains virtually unknown. Certainly, bivalve larvae are likely to be utilized as a food source by other organisms; the consumption of bivalve larvae by amphipods as has been demonstrated using radiotracers by Ejdung and Elmgren (1998) and Ejdung et al. (2000). Bivalve larvae may also act as competitors with other pelagic organisms for resources such as food and settling substrate (Lee and Ambrose 1989).

2.2b Ecological function (Biodeposition and nutrient recycling)

Biodeposition. Bivalves can influence their environment by altering the flow of nutrients and materials. Most filter large amounts of water, removing suspended particulate material which is then incorporated into the animals, excreted in dissolved form or repackaged and released as faeces and pseudofaeces. Faeces and pseudofaeces differ from other seston particles in aggregate size and shape, organic matter content and cohesive properties (Miller et al. 2002). As a result, repackaging induces a downward flux of seston which in turn may alter sediment biogeochemistry and sediment-water nutrient exchange. This may have subsequent feedback effects on the phytoplankton and thus the bivalves themselves.

Biodepostion can result from physical modification of bed roughness and active filter feeding (Miller et al. 2002). In a flow-through system, downstream biodeposit patterns depend on shellfish bed roughness, current speed and seston quality (Miller et al. 2002). Most effects are seen with 1 m of the bed (Norkko et al. 2001; Miller et al. 2002) and may be swamped in highly depositional environments (Norkko et al. 2001). In the field, significant increases in organic matter content and nutrient enrichment have been observed around oyster reefs (Dame and Prins 1998), mussel beds (Prins et al. 1998) and clam beds (Bartoli et al. 2001).

Nutrient recycling. Wild populations of bivalves may exert "bottom up" control on phytoplankton populations by changing rates and processes of nutrient regeneration (Newell 2004). For example, *C. virginica* fed on natural seston assimilated 50% of PON cleared from the water column and the rest was voided as biodeposits (Newell and Jordan 1983). Large amounts of biodeposits reflect a transport of particulate organic matter from the water column to the sediments (Jordan and Valiela 1982) with potential nutrient regeneration. Some of the N absorbed from ingested food is excreted as urine (Bayne et al. 1976; Bayne and Hawkins 1992) that increases the nitrogen pool in the water column, potentially supporting new phytoplankton and microphytobenthos production (Kaspar et al. 1985; Asmus and Asmus 1991; Swanberg 1991). Certainly, measured rates of NH_4+ flux from natural bivalve communities (direct excretion plus regeneration from biodeposits in

the sediments) can be substantial (Dame et al. 1989a; Asmus and Asmus 1991; Dame et al. 1991b; Dame et al. 1992). Based on either direct measurements of phytoplankton production or production potentially supported by measured rates of N flux, these high levels of NH_4+ regeneration are suggested as evidence that bivalve populations may not be able to exert long-lasting top-down control on phytoplankton populations or that bivalves serve to recycle rapidly nutrients, thereby enhancing rates of primary production and phytoplankton biomass (Doering et al. 1987; Dame and Dankers 1988; Dame et al. 1989a; Prins and Smaal 1990; Asmus and Asmus 1991; Dame et al. 1991a; Dame et al. 1991b; Dame et al. 1992; Dame and Libes 1993; Nakamura and Kerciku 2000). Newell (2004) suggests that enhancement, by bivalve biodeposition, of the burial of N and P and removal of N from the ecosystem via denitrification (Newell et al. 2002; Newell et al. 2005) may be often overlooked. In addition, factors such as microphytobenthos abundance also affect nutrient transformations and regeneration (Sundbäck and Graneli 1988; Sundbäck et al. 2000). Using linked flume/tank mesocosms, Porter et al. (2004) studied nutrient regeneration from sediments in response to light and bottom shear. The authors demonstrated that oysters shifted processes to the sediments by decreasing phytoplankton biomass without stimulating additional blooms and by increasing light penetration to the bottom. Light, as enhanced by the oyster feeding on phytoplankton, increased microphytobenthos biomass; a moderate bottom–shear velocity eroded the biomass. Microphytobenthos biomass decreased nutrient regeneration from the sediments to the water column and may have implications for water quality in low-energy parts of shallow-water estuaries. Enhanced bottom-shear in more energetic parts of shallow estuaries negatively affects microphytobenthos biomass and may increase nutrient regeneration from the sediments.

The ecosystem effects of filter-feeding bivalves on sediment nutrient regeneration, and hence on phytoplankton production, will vary depending on bivalve population density and the rate of mixing of oxygenated water down to the sediment surface. Excess biodeposition, especially in low water flow environments, has the potential to stimulate bacterial respiration to such an extent that sediments become anoxic, thereby inhibiting coupled nitrification/denitrification and causing sediment-bound P to be mobilized. Moderate water currents or wave action, spreading biodeposits across a larger bottom area and mixing oxygen from the surface to the bottom waters (Haven and Morales-Alamo 1968; Dame et al. 1991b) can reduce these effects. Water flow may modify the direction and magnitude of process pathways and affect benthic–pelagic coupling (Porter et al. 2004).

Feedbacks between bivalves, phytoplankton and nutrients have been well-studied (e.g. Dame 1996). Indeed, these interactions form the basis of what is commonly referred to as "carrying capacity studies" (see related paper by Chamberlain et al. 2006). It is well known that large standing stocks of bivalves may play an important role in regulating the abundance of phytoplankton in shallow areas. This has been shown for bivalves, including mussels (Prins and Smaal 1990; Asmus and Asmus 1991), oysters (Newell 1988; Dame 1999; Pietros and Rice 2003) and various other species (e.g., Cloern 1982; Officer et al. 1982). Many bivalves are quite plastic in their physiology and may take advantage of increases in the abundance of phytoplankton by increasing filtration rates. These species include mussels and oysters (Newell 2004). Unlike zooplankton, which take time to react to an increase in phytoplankton standing stock (Tenore and González 1976), bivalves are

permanently present in a system and may react swiftly to an increase in phytoplankton abundance.

A number of studies have shown increased remineralization and increased nutrient fluxes from areas with an abundance of bivalves either from the sediments containing high concentrations of biodeposits or directly excreted by the bivalves themselves (e.g., Kaspar et al. 1985; Prins and Smaal 1990). The relative flux of nutrients from bivalves may be even larger than that related to phytoplankton consumed as bivalves feed not only on phytoplankton but also on detritus, zooplankton, and other things in the plankton. Many of these nutrients are directly available to phytoplankton and may thus stimulate further phytoplankton production (Asmus and Asmus 1991), potentially even a net gain in productivity. On a local scale, the importance of these feedbacks are likely a function of coastal topography and its influence on flushing time and the abundance of bivalves within a given site (Archambault et al. 1999).

This plastic response to food availability coupled with a constant supply of nutrients directly or indirectly from bivalves means that an abundance of bivalves in a system may reduce the intensity and extend the lengths of phytoplankton blooms (Herman and Scholten 1990), potentially leading to increased overall primary production in the phytoplankton. Further, Dame (1996) suggests that this may potentially increase the stability and productivity of coastal ecosystems, increasing their functional and structural sustainability. A historic loss of bivalves from some systems through over-fishing or other factors has contributed to the prevalence of eutrophic conditions in many areas around the world. Indeed, this effect alone has been considered sufficient to warrant the reestablishment of native and or exotic species of bivalves into such areas or others where eutrophication is problematic (Haamer 1996; Rice 2000; Anonymous 2004).

2.2c Ecological function (Habitat)

To date, most research evaluating the role of bivalves as habitat has concentrated on oyster beds, especially with respect to their importance as habitats for fisheries or forage species (Coen et al. 1999; Ruesink et al. 2005). There has also been considerable work done to understand the relationship between mussel bed architecture and local biodiversity (see reviews in Suchanek 1985; Seed and Suchanek 1992; Seed 1996). However, mussel bed work has usually been done at relatively small spatial scales within beds whereas the work on oyster reefs is often done taking in larger spatial scale considerations. Little work has been directed at evaluating the importance of the spatial configuration of assemblages of other bivalve taxa. Thus, most of the following discussion is based on the oyster and mussel literature with references made to other groups when possible.

Bruno and Bertness (2001) suggest that bivalves, as foundation species, have a number of ways in which they facilitate or otherwise influence benthic communities. These include 1) general habitat creation, 2) refuge from predation, 3) reduction of physical stress, 4) reduction of physiological stress, 5) enhancement of settlement and recruitment, and 6) increased food supply. In large part this is because some bivalves, particularly mussels and oysters, may transform the structural heterogeneity of the environment such that relatively homogeneous two-dimensional habitats become complex three-dimensional ones (Suchanek 1979; Tsuchiya and Nishihira 1985; Kostylev 1996; Luckenbach et al. 1997; Ruesink et al. 2005). Infaunal and surface dwelling species such as clams and scallops

have less of a direct impact on three-dimensional structure and, consequently, less of an effect as foundation species and as modifiers of the benthic habitat. Each of these elements is discussed below, followed by a discussion of the importance of this habitat for fish and other animals.

Habitat creation. Bivalves make a large amount of shell ($CaCO_3$) with some authors suggesting that they may create permanent physical structure at a rate similar to that of trees in forests (see review in Gutiérrez et al. 2003). Quite simply, bivalves - especially oysters and mussels and especially when creating novel hard habitat in otherwise soft-sediment systems - may significantly alter the physical structure of the benthic environment by their physical presence. That is, they change fairly homogenous two-dimensional environments into complex three-dimensional ones. This includes the surface of the shells themselves, all the nooks and crannies they create, the sediments that accumulate within the matrix, as well as the habitats formed by the associated species (Lohse 1993; Albrecht and Reise 1994). This increases the number and type of habitats available in a given area with concomitant increases in the abundance and number of species (see below). A number of manipulative studies on mussels have also shown that it is indeed the physical structure created by the bivalves that is important and not so much the biological role of the bivalves that modify the structure of the local assemblages as beds of plastic mimics or empty shells of the bivalves develop associated communities similar to those in corresponding natural beds (Suchanek 1979; Ricciardi et al. 1997).

At the smallest spatial scale, the physical influence of any bivalve species will be a function of its shell morphology (size, form) and its spatial arrangement - the extent to which it is aggregated (Gutiérrez et al. 2003). At the level of individual bivalves, large shells generally host a greater number and number of types (Keough and Butler 1983; Giacobbe 2002) of organisms than do small shells. This is probably due to both the space available for colonization and to the greater age of larger bivalves. Similarly, larger empty shells may also provide refuge for more species than do smaller ones. All else being equal, the more rough or ornate mollusc shells are the greater the chance there is for colonization (Giacobbe 2002) via modification of current fields (Bourget et al. 1994; Grégoire et al. 1996) or provision of the appropriate microtopography for settlement (Johnson 1994; Miron et al. 1999) and thus the greater should be the diversity of the communities that develop on them. The proportion of the bivalve that is exposed is also of importance to the development of an associated community. An interesting example of this comes from New Zealand where the cockle *Austrovenus stutchburyi* is an abundant bivalve in sheltered coves. The bivalve normally lives buried in sediments but when infested by a parasite cannot bury itself and lays on the mud surface, increasing local species diversity by providing the only hard substrate in the mudflat to organisms that need this (Thomas et al. 1998; Thomas et al. 1999).

At a larger scale - that of individual beds - the spatial configuration of bivalve communities within the environment has a great influence on local assemblages. Spatial configuration is largely a function of the groups involved. As outlined above, there are four basic types of spatial configuration: buried in unconsolidated sediments (clams), cemented onto hard substrates (oysters), attached to the substrate by byssal threads (mussels), and free-living on the bottom (scallops). But there is also great variation among these different groups for different taxa and within taxa under different environmental conditions. On average,

oysters create the most physically complex habitats, with historic *C. virginica* reefs measuring up to 3 m high (Lenihan and Peterson 1998). In fact, of all oyster species, this one develops the most expansive and complex reefs although other species may develop to form a more heterogeneous mix of shell and sediment (see discussion in Ruesink et al. 2005). Large changes in structural complexity as associated with oyster reefs will modify hydrodynamics (Breitburg 1999; Kennedy and Sanford 1999) with cascading effects on a variety of processes (e.g., food and recruit delivery) that may influence the habitat indirectly (Jumars and Nowell 1984; Sebens 1991; Breitburg et al. 1995; Eggleston et al. 1999). Modification of local hydrodynamic regimes is also important at smaller spatial scales. For example, Green et al. (1998) showed that both the horse mussel *Atrina zelandica* and cockles on the bottom modify drag and skimming flow and that, at a smaller scale, the orientation of the mussels is important in determining both of these measures. Cummings et al. (2001) did a manipulative experiment and found that the density of *A. zelandica* influenced the structure of infaunal communities but these differences varied temporally and spatially. Also at a small spatial scale, variation in shell layer thickness and the proportion of whole shells may also influence a number of ecological processes for both oysters (Iribarne 1996) and mussels (Suchanek 1979).

Refuge from predation. The many nooks and crannies within bivalve beds serve as refuges from predation for a variety of invertebrates and fish species (Gutiérrez et al. 2003). For example, Bartol and Mann (1999) discuss the importance of interstitial spaces as refugia from predation for oyster spat and Coen et al. (1999) point out the same space also protects small fish from larger piscivores. Arnold (1984) reports that the quahog, *Mercenaria mercenaria*, is less vulnerable to predation by crabs when associated with oyster shells. Although not the focus of the study, Suchanek (1979) also reported fishes from intertidal mussel beds in Washington (even at high tide!) and rock gunnels, *Pholis gunnellus*, are often seen on mussel beds in eastern Canada, quickly seeking refuge within the mussel matrix when scared by scuba divers (McKindsey, pers observations). Even infaunal bivalve species may create a refuge from predation. Skilleter (1994) showed that the bivalves *Mya arenaria* and *Macoma balthica* are both given a substantial refuge from predation by crabs when associated with the infaunal bivalve, *Rangia cuneata* and Peterson and Black (1993) found that the predation rate of starfish was negatively related to cockle density as dense beds of the bivalves lowered starfish foraging efficiency. Thrush et al. (2002) sampled a number of habitats on soft sediments and found that habitat structure in the form of scallops and horse mussels had a positive influence on the abundance of juvenile snapper, suggesting that it acted as a refuge from predation. In a series of observational and manipulative studies, Dolmer (1998) showed that starfish preying on mussels forage less efficiently as the structural complexity of a mussel bed increases.

Physical stress reduction. One of the most obvious physical stresses in the marine environment is the physical force exerted by the water itself on the organisms (Denny 1994; Helmuth and Denny 2003). This is especially true in intertidal areas where the full force of waves may crash on the shore. Nonetheless, mussel communities flourish in this habitat and a plethora of species live associated with mussels, protected from the full force of the waves within the mussel matrix (Seed and Suchanek 1992; Seed 1996).

Physiological stress reduction. Living within the mussel matrix also reduces thermal stress as the mass of mussels modulates temperatures relative to those outside of it

(Helmuth 1998) as well as regulating humidity levels and thus reducing desiccation (Suchanek 1985). This is also of importance in soft sediments as Gutiérrez et al. (2000) suggest that the stout razor clam, *Tagelus plebeius*, may also protect small organisms from thermal stress.

Settlement and recruitment enhancement. Recruitment of larvae from the plankton to the bottom may be via passive or selective processes or a combination of both (Eckman 1983; Butman 1987). The larvae of many species act basically as passive particles in the water column (Hannan 1984; Gross et al. 1992). As discussed above (Habitat creation), settlement and recruitment of these species may be enhanced at a small scale by bivalve shells modifying hydrodynamics and thus propagule delivery rates (Bourget et al. 1994; Grégoire et al. 1996). Once on a substrate, microhabitat selection of larvae is also possible (Gross et al. 1992; Lemire and Bourget 1996; Miron et al. 1999; Olivier et al. 2000) and many species actively select the sort of habitats that bivalves and bivalve beds and their associated flora and fauna provide (Matsumasa and Nishihira 1994). This is especially so for larger species, such as fishes and decapods (Breitburg et al. 1995; Breitburg 1999; Posey et al. 1999), although hydrodynamic modification by bivalves reefs and other sources of heterogeneity remain of importance at larger spatial scales (Butman 1987). For example, Breitburg et al. (1995) studied the settlement of the naked goby, *Gobiosoma bosc*, larvae within oyster reefs in Chesapeake Bay and found that larvae accumulated downstream and in the wake of large sources of heterogeneity (oyster-covered rocks) in the reefs and that settlement reflected this pattern. The authors point out that the larvae were not acting as passive particles in this case and were swimming actively against the currents.

Increased food supply. Bivalves and bivalve beds increase food supply in much the same way that they provide refuges from predation and enhance settlement and recruitment. The most obvious way in which they increase the food in the system is that they themselves are food sources for a good number of predatory taxa including flatworms, gastropods, starfish, urchins, decapods, fish, birds, mammals (Meire 1993; Seed 1993; Dame 1996). Bivalve larvae may also constitute a large proportion of the diets of filter-feeding organisms such as ascidians, barnacles, and other bivalves (White and Wilson 1996). Bivalves have been reported to consume larvae of the same species (Dame 1996), however, ingestion is most likely a passive function of individuals filter-feeding adjacent to those spawning and not selective predation. Further, the variety and abundance of associated flora and fauna provides another source of food for a variety of other species. Modification of benthic hydrodynamics by mussel beds has also been shown to influence the delivery of phytoplankton to the benthos (Fréchette et al. 1989), augmenting the food supply to all the consumers that rely either directly or indirectly on this food source.

Diversity, abundance and productivity. Many factors contribute to the areal diversity and productivity associated with bivalve beds. An evaluation of the diversity of the assemblages associated with bivalve communities is a simple way of showing their importance to the functioning of the system. Typically, the bigger the patch, the greater the associated diversity (Tsuchiya and Nishihira 1985; Coen et al. 1999; Eggleston et al. 1999). Similarity, diversity of the associated species in mussel beds is positively related to bed thickness (Suchanek 1979). That being said, Hammond and Griffiths (2004) report that *M. galloprovincialis* bed thickness is greatest on intermediately exposed shores in South

Africa whereas the diversity of associated organisms is maximum in the most and least exposed sites. The density of bivalves may also influence various measures of associated community structure. Commito and Boncavage (1989) modified the density of *M. edulis* on a soft-bottom community and found the abundance of infauna (the oligochaete *Tubificoides benedeni*) to be positively correlated with mussel density. They suggest that this correlation may result from the greater abundance of food for the oligochaetes (mussel faeces) in areas with a higher density of mussels. Similarly, Dumbauld et al. (1993) found juvenile Dungeness crab (*Cancer magister*) survival to be greater on experimental plots with either a heavy layer or scattered piles of oyster shells than in plots with only a light cover of shell.

For mussels, the most diverse communities are associated with the Pacific mussel, *Mytilus californianus*. Suchanek (1979) reported over 300 species of invertebrates, fishes and algae from *M. californianus* beds in Washington and Kanter (1985) has listed over 600 species of invertebrates and 141 species of algae from sites with *M. californianus* beds in Southern California with a maximum of 174 and 23 species, respectively, from a single site. In Australia, Peake and Quinn (1993) observed up to 44 species associated with the mussel *Brachidontes rostratus* and Jacobi (1987b; 1987a) has found 15 classes of organisms associated with the mussel *Perna perna* in Brasil, including up to 15 species of amphipods in a single site. With respect to the mussel *M. edulis*, the species with the widest distribution (Seed and Suchanek 1992), Briggs (1982) reported over 30 associated species in an Irish soft sediment community whereas Asmus (1987) and Kröncke (1996) have reported over 40 and 14 associated species, respectively, in soft sediment communities in Germany. On hard surfaces, Tsuchiya (1979) suggests that there are 20 species that form the base a community studied in Japan but that many others are present. Others studies by Tsuchiya in Japan (1985; 1986) have reported 24 and 45 associated species and Kostylev (1996) found up to 14 associated species in 0.01 m^2 samples in Sweden. The *M. edulis*-associated communities in eastern North America are less diverse and well known (Menge 1976). In soft sediments, Commito (1987) found only 10 associated species in Maine whereas Newcombe (1935) found over 60, although this high number is likely related to the very large area sampled (10 m^2). In a series of studies on *M. edulis*-associated communities on rocky shores in the Gulf of St. Lawrence, Mckindsey and Bourget (2000; 2001b; 2001a) found a mean taxonomic richness of about 10 species per 0.01 m^2 sample although the patterns observed were highly dependent of the size of the animals considered in the calculation of richness. A similar review of the diversity of invertebrates associated with oyster beds is also possible (and has been largely done, see Lenihan and Peterson 1998; Breitburg 1999; Ruesink et al. 2005) but would not advance any new information and so will not be repeated here.

The importance of oyster reef habitat for fish and macroinvertebrates such as crabs and shrimp seems fairly well established (Breitburg 1999; Coen et al. 1999). In a recent study that estimated the enhancement of fish production through restoration of oyster reefs in the south-eastern United States, Peterson et al. (2003) compared the abundance of 5 species of large mobile crustaceans (crabs and shrimp) and 48 species of fish on oyster reefs and mudflats. They found that the abundance of 19 of these species was enhanced by the presence of oyster reefs with the abundance of a further 9 species also likely being enhanced but that there was insufficient data to fully support this conclusion. Of the 19, 10 were limited in recruitment by habitat area (termed recruitment-enhanced), and 9 limited in

production by reef refuges from predation and available food (growth-enhanced). Similarly, Coen et al. (1999) reviewed studies done on 7 reefs in the same areas and divided reef fish into 3 categories: i) reef residents (using the reef as a primary habitat), ii) facultative residents (generally associated with structured habitats with vertical relief or shelter), and iii) transient species (foraging on or near the reef but also wide-ranging). Of the 79 species thus classified, 7 clearly fell into the first class and 5 others also reproduced within the reef complex. Of the remaining species, many, including both recreationally and commercially important species, also spend prolonged (months) periods on the reef and many species classified as transient are also more than likely actually facultative (Coen et al. 1999). What's more, within single reefs, resident species accounted for 9-36% (mean = 21%) of the total number of fish species present. However, recent work by Grabowski et al. (2005) shows that the magnitude of enhancement of invertebrate and fish biomass relative to control sites is habitat-dependent such that the effects are significant when oyster reefs are compared to adjacent mud flats but not when compared to adjacent eelgrass beds.

It must be stressed however that this review has thus far focused on diversity and not productivity. As previously discussed, suspension feeding bivalves act as a link between the phytoplankton and other food sources in the water column and thus there is an obvious reason why bivalve beds should logically increase the secondary productivity of the local environment. Consequently, a number of authors have suggested that bivalve beds may increase local secondary productivity. Cusson and Bourget (2005a) review much of the work to date examining the productivity of mussel (mytilid) populations and find this suggestion to be true for the mussels themselves. Wildish and Fader (1998) go one step further and suggest that benthic populations of the horse mussel *Modiolus modiolus* and the associated suspension feeding community represent an extremely productive habitat. Indeed, Asmus (1987) show this to be true for a series of *M. edulis* communities in the Wadden Sea although most of the productivity was associated with the mussels themselves and not the associated species. Nonetheless, Nixon (1971) found the metabolism (respiration) of an *M. edulis* community on a rocky coast in Rhode Island to rival that of any other system measured. Again, most of the biomass of the reef was contained within the mussel fraction of the community. In one of the few attempts to estimate the productivity of fishes associated with bivalve habitats, Peterson et al. (2003) calculated that the restoration of oyster reefs would cause a net gain of fish and macrocrustacean productivity of 2.6 kg yr^{-1} 10 m^{-2}. Finally, mussel communities may have a positive influence on benthic productivity through a variety of cascading effects. For example, much work has shown that filter-feeding bivalves may improve water clarity (Meeuwig et al. 1998; Rice 2001) and Newell (1988) has suggested that improved water clarity due to oyster filtration could be beneficial for benthic micro- and macroalgae. This in turn may influence macrobenthos abundance and productivity.

2.2d Ecological function (Macrophytes)

Macrophyte communities, particularly seagrass communities, are vital to the ecological structure, function, and productivity of aquatic ecosystems. With animals in almost every major phylum represented along with numerous associated species of macroalgae and epiphytes, such communities are the most diverse of the soft-bottom marine communities (McRoy and MacMillan 1977) and combine exceptionally high primary and secondary productivity (Williams and Heck 2001). The structural complexity of these communities

both above and below the substrate function to provide increased growth opportunities (Irlandi and Peterson 1991; Irlandi et al. 1995), predation refuge (Irlandi 1994; Irlandi et al. 1995), increase prey-capture opportunities for ambush-predators, and enhance recruitment success, while increasing sedimentation of suspended particles, cycling nutrients, and stabilizing sediments by decreasing water velocities (Williams and Heck 2001; Newell and Koch 2004). Seagrass communities also function as nursery areas for a variety of organisms, particularly various life stages of many commercial fish species, by providing opportunities for increased growth and survival (Heck et al. 2003). Macrophyte communities are also critical for supporting waterfowl populations which may feed heavily or almost exclusively on seagrass (Seymour et al. 2002; Hanson 2004). For these reasons, much scientific attention and effort have been invested in recent years to understand anthropogenic alterations to macrophyte communities as well as introduce restoration efforts to mitigate our influence on these communities.

Natural aggregations of suspension-feeding bivalves are capable of positively interacting with macrophyte communities in a variety of manners. By filtering large quantities of particulate nitrogen which is remineralized as ammonium and made available for plant growth, suspension-feeding bivalves are part of a positive feedback loop which can increase nitrogen cycling rates (Dame et al. 1984; Dame et al. 1989b). Bivalve fecal matter also contributes considerable amounts of phosphorous to sediments (Dame et al. 1989b) which then promotes phosphate releases from sediments under anaerobic conditions (Nixon et al. 1980), thus potentially encouraging plant growth. Such positive reactions have been recorded between natural bivalve populations and seagrass. Cord grass (*Spartina alterniflora*) production was shown to increase in the presence of ribbed mussels (*Geukensia demissa*) (Bertness 1984) while Reusch et al. (1994) reported a doubling of sediment concentrations of ammonium and phosphorous as a result feces and pseudofeces deposits by mussels (*M. edulis*) and suggested this may fertilize the growth of eelgrass *Zostera marina.* Peterson and Heck (2001), however, were the first to experimentally address these mechanisms. As well, these authors further hypothesized bivalves could also enhance macrophyte growth and productivity by indirectly reducing epiphyte abundances via the creation of three-dimensional shell structure, thus providing refuge from predation for grazing species such as small gastropods or amphipods. Plots of *Thalassia testudinum* were treated with densities of 0, 500, and 1500 *Modiolus americanus* m^{-2}. In mussel plots, sediment concentrations of total nitrogen and phosphorous doubled and C:N, N:P, and C:P ratios in plant tissues decreased significantly, demonstrating that these bivalves increased sediment nutrient content and these nutrients were utilized by the seagrass. Leaf lengths and net primary production were also significantly greater in mussel treatments. While mussel treatments of *T. testudinum* also had significantly lower epiphyte loads, no significant difference in grazer abundance was noted among treatments or controls. While the grazer results were not expected by the authors, this experiment clearly demonstrated a positive influence of a suspension-feeding bivalve on macrophytes.

3. OVERVIEW OF BIVALVES IN AQUACULTURE

As pointed out previously (see Table 1), there are many steps involved in most types of bivalve aquaculture and these vary greatly among the species, among regions, and among individual producers. Much of this information is already readily available in the pertinent literature and will only be summarized here. Because of broad differences between the regions, we have divided the discussion to treat the east and west coasts separately.

3.1 Overview of bivalves in aquaculture (East Coast)

The bivalve culture industry on Canada's east coast is dominated by the blue mussel (*Mytilus edulis* and varying amounts of *M. trossulus*), followed by oysters and then scallops with lesser numbers of other species also being raised. On the whole, most species being cultured are indigenous and spat are obtained through natural set, the juveniles usually being transferred to grow-out sites distant from areas in which they were collected. General information about culture methods for both of these two species may be obtained from DFO websites (Fisheries and Oceans Canada 2003b, 2003a) and information about these operations is only summarized below.

Mussels. Mussel aquaculture is practiced around the world using two main approaches: bottom culture, which accounts for approximately 15% of the overall production, and suspended culture, which accounts for about 85%. Although bottom culture is presently used in the US, it is mainly practiced in Europe, particularly in the Netherlands, Germany, Ireland and the UK. In short, the technique consists of transferring juvenile mussels from natural, high density beds, to sheltered beds where the stocking density is managed to improve productivity and market value (Spencer 2002). There are no mussel bottom leases in Atlantic Canada.

Mussel seed are mainly collected in the same bays or water system where the grow-out takes place, but generally on specialized leases in separate section of the bay. For the most part, wild seed is collected on ropes that are attached to long line systems (see below). The ropes are usually 2-6 m in length and are attached at short distances apart (30-50 cm) on a long line that can average 100 m in length (Mallet and Myrand 1995). They are usually deployed in late spring and are retrieved or harvested approximately 5 months later, in late fall for socking activities. A small proportion of the mussel seed used in mussel farming is harvested directly from wild beds. Harvesting in this instance is mainly done using tongs or rakes, in late fall.

Seed collection on artificial collectors has not been linked changes in the recruitment success on wild beds occurring in the same system. The main concern with the deployment of seed collectors is their effect on the recruitment of non-target species. There is also some concern about the high biomass of these filtering animals, certainly as it reaches its highest level, just prior to the recovery of the seed. For instance, in Tracadie Bay PEI, the average seed density (km/m^2) on seed collection leases in the month of October, can exceed the mussel densities on grow-out leases (Landry et al. in prep-a).

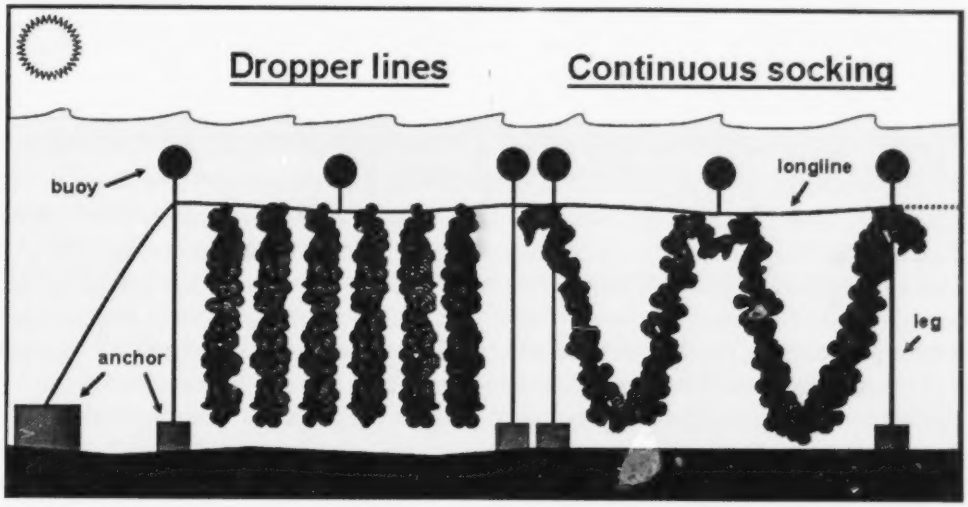

Figure 1. Schematic of a basic mussel longline system. The two most common systems used in Canada are shown. Longline systems may also be used for the culture of other species in nets, trays, etc.

Suspended culture is conducted using three main approaches. In Spain, Scotland and South Africa mussel culture is mainly conducted on rafts (Boyd and Heasman 1998; Okumus and Stirling 1998; Fuentes et al. 2000). This culture technique involves suspending mussels attached on ropes or in socks, typically 8-10 m in length, from a moored raft with cylindrical floats. The bouchots (poles) technique was developed in France (Garen et al. 2004). This technique involves the uses of poles or stakes driven into the ground in regions with high tidal regime. This method is only used in France and is located in shallow water where access is possible at low tide. The third type of suspended culture is the longline system, which is used around the world. It can be used in a wide variety of environment, from the open sea to enclosed areas. Mussel aquaculture was first introduced in Atlantic Canada, on PEI in the late 1970's. From it's beginning, the off-bottom long line was the preferred technique and is now sole method of culture on the island. It consists of a series of lines anchored at both ends and floated in the water by buoys with a series of "legs" with weights at their ends, usually cement blocks, as counter balance (see Figure 1). The number of each is varied throughout the year and their length adjusted to maintain the growing bivalves at the appropriate level in the water column to maximaize growth and minimize impacts from fouling, ice, etc. Mussels are hung along the line in mesh socks typically around 3 m in length. The long line can vary in length from 100 m up to 200 m. (Mallet and Myrand 1995). During the winter period, the long lines are sunk deeper in the water column to avoid ice damage. The system is similar in the Magdalen Islands except for the fact that continuous socking methods are used. In Newfoundland, culture sites are typically deeper and both methods are used.

The American oyster. The American oyster, *Crassostrea virginica*, is naturally found along the Atlantic coast of North America. Along the Atlantic coast, this species is

common from Cape Cod, Massachusetts to the Gulf of Mexico with large populations found at the northernmost portion of its distribution in the southwestern Gulf of St. Lawrence (Lavoie 1995). In the Maritimes, oysters have traditionally been cultured to market size (76 mm in length) seeding and growing oysters directly on the substrate (bottom culture) or by growing oyster seed in plastic mesh bags on tables or trestles approximately 30 cm above the substrate (off-bottom culture).

Bottom culture in the Maritimes is predominantly conducted in low intertidal and subtidal areas (up to 5-8 m in depth) with moderately soft substrates. Such areas are generally regarded as the best locations for bottom seeding as the substrate provides adequate shell support which results in oysters growing strong, round shells that have high market appeal. Once seeded in an area suitable for growth as well as protection from winter ice exposure, bottom culturing requires little care other than monitoring growth and survival and presence of predators or fouling organisms. Upon reaching market size (approximately 4-7 years in the southern Gulf of St. Lawrence), oysters are most commonly harvested by small boat using tongs or drags. In some areas, large boats with high-powered engines towing heavy drags are used for harvesting which can result in severe bottom damage and losses of product (Lavoie 1995). Less destructive alternatives such as diver harvesting are used, but are the exception as it is generally cost-prohibitive to harvest in this manner.

With off-bottom culture, oysters are contained in plastic mesh bags which are then attached to metal or wooden tables or trestles in the low intertidal or shallow subtidal zones. The combination of raising oysters above the substrate and placing them in bags acts to decrease predation while exposing the oysters to increased water circulation, improving growth and elevating the organisms above areas of substrate where anoxic events may occur. In the Maritimes, harvesting of sub-tidal leases is generally done from barges with trestles or racks mechanically lifted on to the barge resulting in little bottom disturbance. Alternatively, intertidal harvesting from racks or trestles involves increased vehicular and foot traffic in the intertidal zone.

Early attempts at suspension culture involved many different techniques. Spat were traditionally collected on scallop shells suspended through the water column on strings from wooden racks. Some growers would leave spat to develop on these shells where they were capable of reaching market size within two years by taking advantage of warmer water temperatures and higher primary productivity of the upper water column (Lavoie 1995). Similar methods included the suspension of wooden or stacked plastic trays. Drawbacks of these early attempts were related to the increased cost of suspension infrastructure materials and product quality. Much effort and cost are required to construct suspension structures which can withstand Maritime weather events. Further, increased labour costs generally result from efforts to keep suspended structures free of algal and other biological fouling which reduce water circulation and impair oyster growth. In terms of product quality, the increased growth rates of suspended oysters resulted in thin shells which often could not withstand shipping rigors or were difficult to open without breaking. To counteract this dilemma, growers were forced to spread oysters on the bottom for a period to increase shell strength, raising labour costs. All of these factors combine to decrease the marketability of a competitive product and led to cessation of this culture approach in the mid-1990's (Lavoie 1995).

Today, seed supply for oyster aquaculture in Atlantic Canada comes from two main sources. The first is through the collection pre-commercial oysters from wild contaminated beds for relaying operations on private leases (Lavoie 1995). Collection of these pre-commercial oysters is mainly done with the use of thongs. This form of aquaculture is still active, but represents a decreasing proportion of oyster production in Atlantic Canada, particularly in N.B. The second source of oysters for aquaculture operations is though the collection of seeds, which are solely collected on artificial collectors. Harvesting of oyster seeds on wild beds is not permitted. These artificial collectors usually consist of a wide variety of plastic surfaces covered with a thin coat of cement. Oyster and other bivalve shells held in mesh bags are also used for collecting seeds in some areas. These collectors are deployed in the water column either on a long line system (see above) or on a wooden fence system. Deployment occurs in early summer and the collectors are usually retrieved in the fall for thrashing (removal of individual seeds for the plastic collectors) or they are directly deposit on the bottom, in water safe from ice damage, for the winter month and thrashing in the spring.

New developments in culture technology and market demand, however, have led to the adoption a new suspension technique used for rapidly growing smaller, cocktail-sized (approx. 50 mm) oysters. While still extremely rare in Prince Edward Island and moderately rare Nova Scotia, over 85% of active New Brunswick oyster leases have abandoned bottom and off-bottom culture and adopted this new technique (R. Dupuis, New Brunswick Department of Agriculture, Fisheries, and Aquaculture, *pers. comm.*). Using this method, lines of plastic mesh bags (similar to those used by off-bottom growers) are suspended at or just below the waters' surface in the shallow subtidal zone using styrofoam or plastic floats attached to the bags. The ends of these lines are anchored to the substrate and measure approximately100 ft. In general, bags measure approximately 2-3 feet long by 1 foot wide and are 3-4 inches deep and may be floated in single or double rows (A. Levi, Elsipogtog First Nation, *pers. comm.*). In certain regions, growers float multiple bags (two across by two deep) in metal cages to increase the number of oysters cultured per unit area (M. Skinner, *pers. obs.)*. Lease sizes in the Maritimes range from 3.51-15.71 ha with an average of 4.01 ha (Fisheries and Oceans Canada 2003a). With this method, oysters grow to cocktail size in 3-4 years. Oysters grown to cocktail size in this manner are generally kept at lower densities than oysters grown using other techniques. Lower densities and the movement of oysters back and forth in bags due to wave action contribute to the production of thick, round shells which high meat quality (Fisheries and Oceans Canada 2003a). After reaching a desired size, the bags are removed from the longlines by workers using boats resulting in little or no physical disturbance of habitat.

Scallops. Two species are involved, the "giant" or "sea" scallop, *Placopecten magellanicus, and the* Iceland scallop, *Chlamys islandica*. Scallop spat are obtained using collectors (nylon sacs stuffed with some filamentous material such as nylon mesh to which the recruiting scallops attach with byssal threads). Once the scallops grow to a sufficient size to live a free-living existence, they detach themselves from the recruiting material only to be trapped by the mesh of the collector bag in which the filamentous collecting material was placed. The juvenile scallops are then placed in some type of cage (often pearl nets, several strung together and placed in a long-line grow-out system, but experiments are also being done to evaluate the use of trays, tables, etc.). These are then grown to "princess" size for consumption on the half-shell or then released into the environment for sea

ranching or else to full market size. There is also limited culture of the introduced Bay scallop, *Argopecten irradians*, in Prince Edward Island.

Others. Clam culture in Atlantic Canada is not fully developed. The main species that are being considered for aquaculture are the northern quahog (*Mercenaria mercenaria*) and the soft shell clam (*Mya arenaria*). For both species, nursery systems such Vexar bags or field up-wellers (see below) are used for the first spring and summer months of the growout cycle. In the fall, juvenile calms are either seeded directly on intertidal to subtidal bottom leases for the remainder of the growout cycle or can be overwintered in Vexar® bags for planting in the following spring. Predator nets may be used for the first year. Small *M. arenaria* may also be relayed to grow-out sites to improve growing conditions and shorten grow-out times.

3.2 Overview of bivalves in aquaculture (West Coast)

The bivalve culture industry in western Canada is very diverse with a number of species being cultured in a number of ways. The state of the industry there is very well described in Jamieson et al. (2001) and Kingzett et al. (2002) as well as on the industry website (http://www.bcsga.ca). The following is largely a summary of what is presented in these sources.

The most important bivalve species being cultured in British Columbia are a suite of non-indigenous species, the Pacific oyster (*Crassostrea gigas*), the Japanese weathervane scallop (*Patinopecten yessoensis*), and the manila clam (*Venerupis philippinarum*), the former two having been introduced intentionally and the latter arriving as a hitchhiker with *C. gigas*. (See Landry et al. 2006 for a general discussion of the implications of exotic species in bivalve aquaculture.) Other species being cultured include both the blue and Mediterranean mussels (*M. edulis* and *M. galloprovicialis*, respectively, also both exotic species), geoduck clams (*Panope generosa*), the heart cockle (*Clinocardium nuttallii*) and the European flat oyster (*Ostrea edulis*), a further exotic species. Most of this industry is based on hatchery-reared seed although a variety of methods are used by farmers to enhance natural set and survival. Below, we briefly outline the methods used for culturing each of these species.

Pacific oysters. As in most of the world, *C. gigas* is the most important cultured bivalve species in British Columbia. It is grown using a variety of methods but the trend is towards more deep-water (suspended long-line and raft culture) ones because of the ease of mechanised methods and greater growth rates 2-5 years for beach culture vs 1-3 years for suspended culture). Because of unreliable set, most of the industry is based on hatchery-raised larvae or seed. Eyed larvae are set (undergoes metamorphosis into juveniles and, in the case of oysters, adheres to a substrate where they will grow-out) onto culch (a substrate to which the larvae will accept to settle, often old oyster shells or tubes used for grow-out) either directly at the hatchery or elsewhere (i.e., remote setting at the farm site). "Single" seed is produced by setting onto ground shell fragments in downwellers at the hatchery or setting facilities. Nursery rearing of single seed (over 2 mm) is often done in floating upwelling systems (FLUPSY-a floating structure with bins with screened bottoms and tops, through which natural seawater flows and keeps the bivalve within them more or less suspended). Such seed may also be bought commercially, as can larger seed that is suitable for being transferred directly to tray systems for grow-out. Oysters on shell culch

or tubes may also be transferred to deep-water systems for grow-out or else upgraded to "singles" for the half-shell market. Single shells may also be placed in bags or cages that may also be suspended in suspended systems or placed on beaches or tables grow-out.

Grow-out may be done in a number of ways, based on the type of seed acquired and individual farmer preference. The least involved system is simply spreading out culch oysters on a beach for grow-out. This may involve a number of possible modifications of the beach area, including setting up fences, creating berms (breakwaters) removing large rocks and debris, and possibly tilling. Depending on the type of substrate on a given beach, oysters may also be grown-out in Vexar® (rigid plastic mesh) bags or Aquamesh® (wire mesh with PVC coating) cages directly on the beach or on racks, on stakes, or long-line systems. The mesh size used is the largest possible to avoid losing the bivalves and to ensure maximal water flow. Bags and cages placed directly on the bottom must be staked in place and turned over from time to time to prevent excessive fouling. In areas with softer sediments, bags and cages are typically placed on trays made of rebar. Although large individuals may be placed directly into bags or cages, smaller seed may first be placed in bags with smaller mesh inside of bags and cages with larger mesh size and then split and sorted as they grow. Many of the beaches historically used for oyster culture are now being used for clam culture as the oyster industry moves more off-shore.

In deep-water systems, racks may be constructed that hold several layers of bags or cages. These are most often suspended from rafts or long-lines. A good discussion of the different tray types is presented on the industry website. Individual shell culch with the associated growing oysters may also be inserted into the strands of ropes and used in suspended culture. Tube culture uses 2 m corrugated plastic tubes with a 25 mm diameter that oysters accept as appropriate material to settle on. New tubes must be conditioned, usually in the intertidal area, for up to one year to leach out chemicals and allow the development of an appropriate (for spat settlement) microbial community. The tubes are placed in a tank to allow the larvae to set and then transferred to nursery rearing system and then to a grow-out site after a couple of months. Grow-out is either on long-lines or rafts, with 2-3 tubes often connected together.

Manila clam. The manila clam is another widely farmed bivalve and has recently become the second-most important bivalve species being cultured in British Columbia. Although now fairly widely distributed in southern BC, unreliable recruitment means that the industry relies on hatchery-raised spat or seed. Either larger seed are or else eyed spat are purchased from commercial sources, the latter being raised for a brief period by the growers in FLUPSY systems until large enough to de seeded into grow-out sites. All clams beyond 20 mm are grown intertidally on beaches with specific types of sediments (stable, loosely packed mixture of gravel, sand, mud and shell). Modification of lease sites to enhance clam growth and survival may be considerable. For example, low boulder berms may be established seaward of the sites to reduce waves, gravel and/or crushed oyster shell may be added to make the substrate better for the clams (Jamieson et al. 2001). Prior to seeding, lease sites are first dug to remove any clams present. Seed is planted at size of 5-8 mm at a rate of about 200-600 m^{-2}. The seed is often covered with plastic netting (car cover) to protect it from predation and from being advected away by currents. This netting may become fouled and measures taken to address this problem. Predator removal is also a common practice with clam culture. Beaches may also be tilled throughout the production

cycle during transplantation, thinning and redistribution and harvesting. Harvest at present is exclusively by hand digging although mechanized harvesters have been tested.

Japanese weathervane scallop. As with mussels, the scallop culture industry is fairly recent and entirely based on hatchery-raised spat which are ready to set at about 3-4 weeks under hatchery conditions. The scallops are commonly set in the hatchery on appropriate settlement material (e.g., kinran) inside of mesh bags. These "seed bags" are then transferred to nursery ponds or grow-out sites for nursery rearing. The bags are set to down lines at a rate of about 1 bag m^{-1} and left to grow until they measure about 1.5cm and detach from the settlement material, becoming trapped within the bags (mid-summer). At this time, the scallops are then sorted and placed in pearl nets that may be stacked to about 15 deep, until they reach about 3 cm (September). Following this, they are graded once more and either placed in lantern nets (staked to about 10 deep) or else ear hung (hung from the corner of their shells). Grow-out is in about 1.5-2 years.

Mussels. The mussel industry in BC is fairly new, and is based on hatchery-raised spat. Seed is usually purchased at a size of 1mm or at a larger size after being raised on screens. Alternately, some growers are also experimenting with raising their own seed which is set directly on twine that is then wrapped around ropes for grow-out. Purchased seed is placed in framed screens and, once hard set, put in mesh bags and suspended on long-lines for 2-3 months. The seed is then loaded into cotton tubing and this is wound around ropes for either continuous socking or else on dropper socks, usually in the fall. Both rafts and long-line systems are being used at this time and grow-out is usually accomplished within about 1-1.5 yrs following socking.

Geoduck clam. This is one of the indigenous species being cultured in British Columbia. The geoduck is the largest bivalve in British Columbia with a high market value and thus has a good potential as an aquaculture species. However, subtidal culture of this species is still in transition from the experimental to the commercial phase. All seed being used is from commercial hatcheries and is usually supplied at about 3-6 mm for outgrowing. Nursery areas are subtidal (tables), floating (tables), or land-based (concrete raceways filled with sand) and the clams stay there for the following 9-11 months until they reach a size of 12-20 mm. This seed is then planted mechanically subtidally where it grows to market size (0.7-1 kg) over the following 5-7 years. As with manila clams, geoduck clams are often covered with netting to avoid predation. Harvest is by scuba or hooka diving with divers using pressurized water jets to remove the clams. Intertidal culture of geoduck is well-established in Washington State but is currently done only on a small-scale in BC.

Others. The heart cockle is a further indigenous species with prospects of being cultured in British Columbia. Grow-out techniques for manila clams may be used for cockles. However, the species is not being cultured commercially at this time. There is also limited culture of both the European flat (or Belon) oyster, *Ostrea edulis*, as well as increasing interest in culturing the native Olympia oyster, *Ostrea conchaphila*. However, the culture of these is limited and will not be discussed further.

4. BIVALVE FARMS AND THEIR ROLE AS AND ON FISH HABITAT

Much has been written about the influence of bivalve aquaculture in the environment (see, for example, Kaiser et al. 1998; Cranford et al. 2003a; Cranford et al. in prep). However, in large part these reviews have concentrated on the influence of suspended bivalve culture on the benthic environment, mostly concentrating on the physical, chemical, and biological processes occurring in the sediments. As pointed out by Brooks (2000), the response of the communities on the bottom is much different from those growing associated with the bivalves (and the associated structures) in suspension. The benthic processes are largely a reaction to increased organic loading whereas the water column processes are largely a function of physical structure and filtration activity. Some of these interactions are summarized in Figure 2. The following discussion is thus divided to reflect this. Similarly, the influence of bottom culture differs greatly from suspension culture and thus this section is also treated separately. As interactions with the water column (i.e., phytoplankton-zooplankton-detritus-nutrients) and the benthic infauna are discussed at length in companion papers to this work (Chamberlain et al. in prep; Cranford et al. in prep), these will only be addressed briefly here.

4.1 Bivalves in suspended culture

4.1a Bivalves in suspended culture (water column effects)

Deposition. The extent and magnitude of sediment loading around suspended or bottom cultures of shellfish will depend on both the size of the farm and the hydrographic conditions on the lease. Graf and Rosenberg (1997) have estimated that the interception of laterally advected material and increase in deposition of organic material may double the food supply to the benthos. Shellfish have been shown to significantly increase organic matter deposition at sites with low water exchange and dominated by in situ primary production, while at the other extreme, on sites with great water exchange, changes in organic matter deposition may not be significantly above background. Sediments under mussel farms in estuaries in PEI (Grant et al. 2005) and northwest Spain (Leon et al. 2004) show a significant increase in organic matter content but those in fjords in Newfoundland do not (Anderson et al. 2003). In PEI, Miron et al. (2005) show that organic matter and other benthic parameters were not linked to the presence of mussel aquaculture whereas Grant et al. (2005) suggest that there is a link between sedimentation rates and mussel lines in the same area, based on a biodeposition model. Hydrographic regime will also determine environmental response at sites along open coastlines. Hartstein and Stevens (2005) found that organic matter deposition under mussel lines at three New Zealand farms varied inversely with current speed. Crawford et al. (2003) found few sediment effects associated with shellfish farms along an open coast in Australia. Suspended cultures can also act as a sediment curtain, slowing current speed through the farm and increasing sedimentation rates within its boundaries. For example, Plew et al. (2005) measured a 36-63% reduction in current speed through a New Zealand mussel farm.

Filter feeders can influence water column nutrients directly in a number of ways. Firstly, by capturing particulate material from the water column and repackaging it into faeces and pseudo faeces, they can decrease the concentrations of total nutrients in the water column. Harvesting will also act as a net sink for total nutrients from the water column. A modeling

study from Sweden demonstrated a 20% reduction in net transport of nitrogen (sum of total and particulate) out of the Gullmar Fjord due to mussel farms (Lindahl et al. 2005). Lindahl et al. (2005) suggest that increasing the number of mussel farms in the fjord may be a cost effective way to reduce the impact of nutrient loading from sewage treatment plants.

Secondly, by excreting dissolved nutrients as a result of ingestion of particulate nutrients, filter feeders may enhance primary production during periods when the phytoplankton would normally be nutrient limited. This feedback mechanism has been postulated to enhance primary in and around mussel farms (Prins et al. 1998). Changes to dissolved nutrients on mussel farms are however difficult to measure, possibly because of the localized nature of the inputs, turbulence and variable hydrodynamics and the rapid response of the plankton community.

The balance between nutrient excretion back to the water column and nutrient removal via sedimentation and harvesting will depend on numerous scaling factors including, hydrographic features of the system, nutrient supply and seasonality and the biomass of the shellfish on the farm(s).

Nutrient flux. Bivalves in culture may also influence nutrient fluxes indirectly. The consolidation and sedimentation of seston by filter feeders results in increased organic nutrient loading to the sediments. Inorganic nutrients can be recycled back into the water column following decomposition of the sedimented material. Nutrient regeneration rates under shellfish farms are some of the highest measured in marine environments (Prins and Smaal 1994). Even at sites where natural deposition is high and sediments are already organicly rich, mussel farms can significantly enhance the release of inorganic nutrients from the sediments. In coastal fjords of Newfoundland, where natural sediments may have up to 35% organic matter (LOI) sediments under mussel farms can release 5 to 10 times more ammonium than nearby reference sites (Strang 2003). Phosphate release is also enhanced under farms when redox conditions are suitable for phosphorus mobilization (Strang 2003). The reduced conditions under bivalve cultures may also increase denitrification (Kaspar et al. 1985). This process may represent a net loss of nitrogen from the system to the atmosphere. However, the system will shift to dissimilative nitrate reduction in the presence of sulphide with increased organic loading and denitrification rates will then be reduced (Christensen et al. 2003). In addition, increased biodeposition has been shown to reduce the abundance of microphytobenthos under mussel farms in New Zealand (Christensen et al. 2003). Microphytobenthos are common in the sediments Tasman Bay where they reduce the rates and amounts of sediment-water transfer of nutrients. Ammonium efflux is 14 times great under mussel farms where the microphytobenthos is reduced (Christensen et al. 2003).

The effect of regenerated nutrients on the water column and on primary productivity will depend on several factors primarily related to the hydrological regime of the system. In shallow lagoons and well mixed coastal areas, nutrient regeneration may enhance primary production of phytoplankton or macrophytes (Bartoli et al. 2001). At other sites where stratification prevents return of nutrients to the upper water column, effects will be seen only during fall overturn or upwelling events.

Phytoplankton. As outlined above, bivalves in the natural environment may have a considerable influence on phytoplankton communities. Thus, the great quantity of bivalves

in fairly restrained confines of a bivalve culture operation may have a marked influence on phytoplankton population, ultimately influencing the carrying capacity of the local ecosystem for bivalve culture. This point is discussed at length in many works, including the companion paper to this one by Cranford et al. (in prep), and will only be summarized here.

As discussed above, bivalves may also influence the number and intensity of phytoplankton blooms directly through grazing and indirectly by modifying nutrient fluxes. This appears to be the case in the riá de Arosa in Spain, where Tenore and González (1976) have suggested that the mussels in culture there take advantage of the periodic bursts of primary production brought on by upwelling events and continue to provide nutrients to the system to maintain productivity when upwelling is not occurring. In France, Souchu et al. (2001) found that the high density of oysters in the Thau Lagoon were not food-limited during the summer because of the great rate of nutrient fluxes from the benthos stimulating the growth of phytoplankton. Mussel farms have also been suggested to limit the impact of eutrophication in ongoing aquaculture operations in Prince Edward Island (Landry 2002) and for eutrophication-targeted operations in Sweden (Haamer 1996). Bivalve culture may also have another influence on eutrophication insomuch as the bivalves themselves act as a sink for nitrogen and other elements that are removed at harvest. Of course, in the case of more oligotrophic systems, such as off-shore in New Zealand, this may have a negative effect on the system as nutrients may be limiting there (Kaspar et al. 1985). Other portions of the total nutrient pool may also be sequestered in the sediments within and immediately surrounding bivalve culture operations (Hatcher et al. 1994). Despite the possible use of bivalve culture to negate some of the negative effects of eutrophication, Asmus and Asmus (1991) suggest that this is unlikely to be successful because, as metioned above, not only phytoplankton is mineralized and thus the bivalves may end up boosting the primary productivity of the phytoplankton to levels beyond which the bivalves are able to control. Further experiments and very precise modeling are needed to address these issues.

Zooplankton. Although not usually considered in "ecosystem modelling" for bivalve culture carrying capacity studies (but see Dowd 2005; Jiang and Gibbs 2005), a large concentration of filter-feeding bivalves in the water column as is found in bivalve culture operation may have an influence on zooplankton communities in 2 ways. First, the bivalves may filter out an unknown proportion of the zooplankton in an area, including typical zooplankton species as well as meroplankton of fishes and other commercially important species (Gibbs 2004). Dame (1993) suggests that bivalves are largely assumed to filter out mostly small organisms from the water column. For example, Lam-Hoai et al. (1997) and Lam-Hoai and Rougier (2001) reported that the abundance of microzooplankton was reduced in areas with bivalve farming, relative to sites without it, suggesting that this was due to grazing by the bivalves in culture and their associated fauna. However, recent work has shown that bivalves may also be consumers of larger benthic and pelagic organisms (Davenport et al. 2000; Lehane and Davenport 2002). Davenport et al. (2000) showed that 30-35 mm mussels (*M. edulis*) could consume both 300 µm *Artemia* sp. nauplii and 1-1.2 mm copepods in the lab. Field studies reported in the same study found that mussels consumed (based on stomach content analysis) copepods (< 1.5 mm), crab zoeas (2 mm), fish eggs (1-2 mm), and even amphipods (5-6 mm). Subsequent to this, Lehane and Davenport (Lehane and Davenport 2002) showed that mussels consumed organisms up to 3 mm in length and that cockles (*Cerastoderma edule*) and scallops

(*Aequipecten opercularis*) are also capable of consuming considerable quantities of zooplankton, both when suspended in the water column and when on the bottom. The size classes of organisms consumed in these studies suggest that the larvae of most commercial species may be at risk from this type of predation. On the other hand, the risk is species-specific and at least one species, the American lobster *Homarus americanus*, does not seem to be at risk from mussels (*M. edulis*) in suspended culture (Gendron et al. 2003). Also, Horsted et al. (1988) present the results of a mesocosm experiment that showed that *M. edulis* was important in controlling the abundance of tintinnid ciliates and rotifers but not larger zooplankton. Green et al. (2003) showed that, although they exhibit escape responses, the nauplii of 3 common copepod species (ca. 100-200 µm in length) are all susceptible to being captured and ingested by relatively small (ca. 24 mm) *M. edulis*. Further, Zeldis et al. (2004), responding to concerns brought about the rapid expansion of the Greenshell mussel (*Perna canaliculus*) culture industry in New Zealand, found that mussels there were well able to consume a wide range of zooplankton up to 430 µm (the largest size examined).

Larvae. Bivalves in culture have a very high reproductive output. The importance of the addition of this mass of larvae into the receiving ecosystem remains totally unknown. There are obvious possible consequences in the water column as the bivalve larvae will not only act as a source of food to some species but also as competitors for resources. Hard-bottom communities are often recruitment-limited (Underwood and Fairweather 1989) and this large input of larvae and recruitment propagules may have concomitant effects on benthic communities, sometimes with unknown and unpredictable effects (see Landry et al. in prep-b for a review with respect to exotic bivalves in culture). For example, it may cause the development of mussel or oyster beds where none existed before. A recent example of this is the case of *Ostrea edulis* in Ireland where culture of this species has brought about its reintroduction into at least a part of its historical range after being depleted from overfishing (Kennedy and Roberts 2006). Similarly, bivalves in suspension may also influence the community of other meroplankton with other unknown cascading effects on benthic communities.

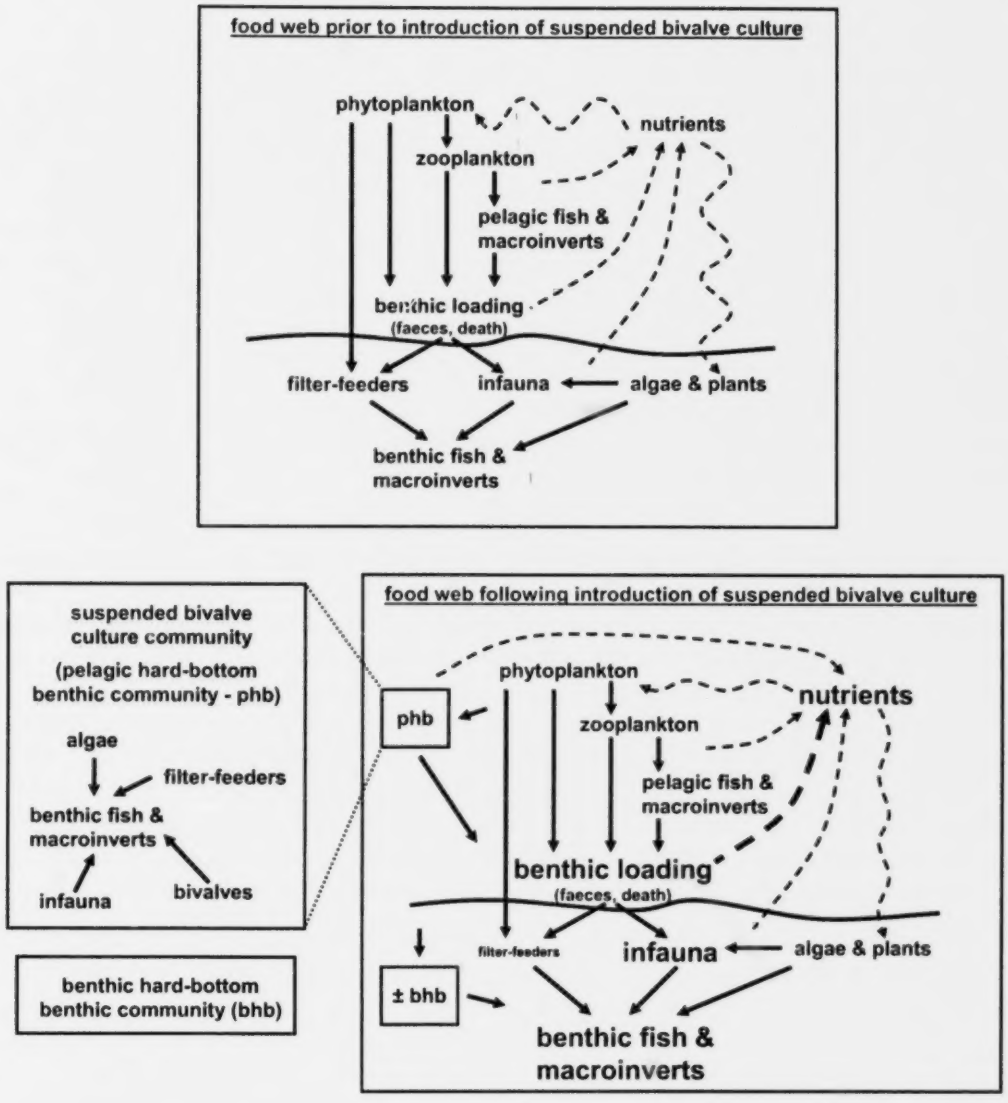

Figure 2. Generalized food webs prior to and following the introduction of suspended bivalve culture. Solid arrows represent trophic links and dashed arrows the flow of nutrients. "Infauna" includes both deposit feeders and predators in sediments. The increase or decrease in font size between the figures shows relative increase or decrease of the size of that component of the community or nutrient flow. Relative variations in nutrient fluxes are indicated by the amplitude of the wave in the arrows. The inclusion of the bhb component is a function of the rate of bivalve drop-off and other factors and may not always be present.

The physical structure of aquaculture sites creates both foraging and refuge opportunities for different species, either directly or indirectly by colonizing species (Shumway et al. 2003). Consequently, it is not surprising that a good number of studies have noted great

abundances and biomass of organisms living associated with bivalves in suspension (Tenore and González 1976; Castel et al. 1989; Khalaman 2001; LeBlanc et al. 2002; Dealteris et al. 2004; O'Beirn et al. 2004). Because suspended cultures act as habitat for fouling organisms the dynamics of dissolved nutrient production and utilization will also be dependant on the type of fouling community. Controlled studies of macroalgae in tidal pools have demonstrated that red algae take up 3 times more ammonium and 4.5 times more total nitrogen when mussels are present (Bracken and Nielsen 2003). Indeed, Lawrence et al. (2000) found that the brown algae *Pilayella littoralis* grows better on mussel lines with living mussels than on control mussel lines with dead mussels, thus supporting the notion that nutrients released from the mussels or their associated fauna increased growth rates. Macrophyte colonizers thus have the capacity use inorganic nutrients excreted by the mussels thereby limiting the feedback of nutrients to water column phytoplankton. Instead nutrients incorporated into macrophytes may ultimately be shunted to benthic communities as plant material drops or is stripped from the lines.

Healthy kelp (*Laminaria longicrursis*) frequently colonize suspended mussel lines in Newfoundland. Kelp are known to store inorganic nutrients during the winter and then use them for summer growth as water column nutrients are depleted by during the phytoplankton bloom (Chapman and Craigie 1977; Gagné et al. 1982). Once their internal stores of nitrogen are depleted they accumulate carbohydrate reserves that are used to support growth at lower light levels once the fall turnover resupplies nitrogen to the upper water column. Under nutrient replete conditions however, they continue to grow through the summer and do not accumulate either carbohydrates or nutrients (Anderson et al. 1981; Gagné et al. 1982). Kelp on mussel lines in Newfoundland show evidence of new tissue growth in both winter and summer (M. R. Anderson pers. obs.) suggesting that the plants are taking advantage of nutrient release from the mussels to grow at optimal rates throughout the year.

In contrast, fouling animals may enhance nutrient release back to the water column if their preferred size classes of prey differ from those of the mussels. Consider for example the invasive tunicate *Styela clava* that has recently colonized many aquaculture sites in Prince Edward Island. Ascidians have been shown to retain picoplankton-sized particles (Bone et al. 2003). *S. clava* has been shown to prefer small (ca 1.5 µm) algae at intermediate temperatures (Zhang et al. 2001). Another fouling tunicate that has recently invaded Prince Edward Island, *Ciona intestinalis*, prefers larger phytoplankton (>16 µm) (Lesser et al. 1992; Zhang et al. 2001). Mussels in contrast mostly select larger phytoplankton (3-5 µm) (Lesser et al. 1992) and frequently consume even larger particles (Karlsson and Larsson 2003). Thus a larger fraction of the particulate load will be consumed by the mussels and fouling community combined than would be the case for mussels alone. Both nutrient excretion and nutrient removal via sedimentation and harvesting (or removal in the case of the tunicates) would therefore be enhanced. However, the degree to which this may occur may not be great as competition studies between mussels and *S. clava* have shown that the presence of the invasive tunicate has little effect on overall nutrient fluxes and phytoplankton consumption (LeBlanc et al. 2002)

Bivalves in suspended culture also act much in the same way as do natural communities of bivalves insomuch as they provide a stable attachment site for the growth of a number of fouling and associated fauna. Indeed, mussel growers are constantly searching for ways to

reduce the abundance of fouling organisms on their bivalves and equipment in order to increase their growth and to facilitate field maintenance and processing (see reviews in LeBlanc et al. 2003; Ross et al. 2004). For example, Leblanc et al. (2003) reported a dozen large and dominant taxa with a total dry weight of about 20g from mussel socks in Prince Edward Island. This was, however, only in the first year of grow-out when epifauna communities are not that developed. In contrast, Tenore and González (1976) found over 100 species on mature mussel socks in Spain and up to 430 g dw of fouling organisms m^{-1} mussel sock. Guenther et al. (in press) reported over 30 species recruiting to pearl oyster valves over a period of 16 weeks. Other work on oyster sites has shown similar patterns. O'Beirn et al. (2004) studied the assemblages associated with floating bag culture for *C. virginica* in Virginia and found a total of 45 (mean = 29) taxa on 50 oysters in each bag with annelids and molluscs being the most abundant groups. Similarly, Dealteris (2004) also studied *C. virginica* in floating bag culture but this time in Rhode Island. They sampled all the organisms > 5 mm in size that were associated with individual 0.6 × 0.6 m cages (containing 12 bags). Over 4 sampling dates (seasons), they found the average number of taxa to vary between about 15 and 23 $cage^{-1}$ and the total abundance of associated species between about 1000 and 2500 individuals. This included 10 fish species, 12 macrocrustaceans, and a number of molluscs, icluding commercially and recreationally important species. Thus, it seems that bivalves in suspended culture function in a similar manner as do natural bivalve beds insomuch as they provide considerable structure, etc, to a system and thus increase local diversity and abundance of organisms.

In sum, with respect to the infaunal and epifaunal organisms associated with bivalve culture, the installation acts more or less like a normal benthic hard-bottom community, what we refer to as a "pelagic hard-bottom benthic community" (see Figure 2).

The organisms growing on bivalves in suspension may in turn attract other organisms, such as fish and more mobile macroinvertebrates. For example, Carbines (1993) found a positive correlation between algal cover and the number of young spotties (*Notolabrus celidotus*) on mussel lines and noted that the fish also associated with encrusting invertebrates and algae on mooring ropes and particularly mooring blocks in New Zealand mussel farms. That these differences were due to the associated species was evaluated and shown to be true with manipulative experiments. Unfortunately, it is unknown whether this effect was due to the fish being attracted by the structure provided by the fouling organisms or to the abundance of associated food items. More recent studies done on mussel farms in New Zealand found a variety of demersal fish species associated with mussel lines; although some pelagic species are also present, they do not seem to make regular use of the farms (Morrisey et al. in press). In Washington, Brooks (2000) suggests that mussel rafts there attract schools of shiner perch (*Cymatogaster aggregata*) that feed on the mussel line-associated community. These observations of generally demersal fishes in bivalve culture sites further support the notion of suspended bivalve culture functioning as a "pelagic hard-bottom benthic community". Using remote methods, Brehmer et al. (2003) examined the distribution of fish and fish schools in a French Mediterranean mussel growing area and found a greater number of fish schools within mussel culture sites than outside of the them. That being said, the schools within the mussel sites were smaller than those outside of them.

Whether or not an artificial reef such as an aquaculture installation actually augments the productivity of the fishes (or other organisms) or serves simply to aggregate them is at the heart of the artificial reef debate (Pickering and Whitmarsh 1997; Bortone 1998; Powers et al. 2003). Unfortunately, most studies of artificial reefs to date have been largely descriptive (Baine 2001; Jensen 2002; Seaman 2002) and there is a lack of rigorous scientific data to support whether artificial reefs have a net positive or detrimental effect on marine ecosystems (Grossman et al. 1997). For example, in one of the few studies that directly addressed the aggregation-productivity issue, Polovina and Saki (1989) examined long-term data for an octopus and flatfish fishery in Japan and concluded that artificial reefs augmented the productivity of the former and only served to aggregate the latter. However, for exploited species, such as those studied by Polovina and Saki (1989), the idea that benthic habitat is limiting is not very likely if fishing effort has already reduced stocks to below the carrying capacity of the environment (Grossman et al. 1997; Powers et al. 2003). An increase in "productivity" may thus simply be a concentration of suitable habitat, the sum of which may have been found elsewhere in the ecosystem. Given this, the only way to show that an artificial reef, such as an aquaculture site, actually increases the productivity of fishes and other assemblages is by showing that their survival and growth is greater on the reef than on the natural habitat on which they are found (Carr and Hixon 1997). To do this, however, is exceedingly difficult experimentally, given the lack of knowledge of the natural history of many of the species involved and the natural variation in the environment (Pondella et al. 2002). That being said, there have been some recent advances to address some of these gaps (Brickhill et al. 2005) although they are still somewhat wanting.

4.1b Bivalves in suspended culture (benthic effects)

Backgound. Of all the influences associated with bivalve aquaculture, the best studied is probably that of the influence of suspended mussel culture on benthic infaunal communities. As bivalves are filter-feeders, they act to repackage small objects (plankton, detritus) in the water column as excrement which sinks at a greater rate, potentially leading to an accumulation of organic matter within and in the general area of bivalve culture sites (see review on mussel biodeposition in aquaculture in Callier et al. in press). Where effects have been observed, they have largely followed the typical eutrophication response model outlined by Pearson and Rosenberg (1978). Briefly, as the level of organic input is increased, typical soft sediment communities dominated by large filter-feeders are replaced by smaller, more deposit-feeding organisms, starting with small polychaetes (notably, the opportunistic *Capitella* spp.), shifting to nematodes, and finally ending up with anoxic conditions and mats of the bacteria *Beggiatoa* spp. (Fig. 3, see review in Rosenberg 2001). These effects have been discussed in detail elsewhere (e.g., Cranford et al. 2003b; Cranford et al. in prep) and will not be repeated here. Here, we briefly summarize what has been reported in these two reviews and concentrate on other studies and factors that have not been considered in those works.

One of the first studies to consider the influence of suspended mussel culture on the benthic environment was that of Dahlbäck and Gunnarsson (1981). They studied sedimentation rates under a mussel lease in Sweden and found that increased sedimentation rates there (relative to a control site) led to an accumulation of organic matter and greater sulphate

reduction and sulphide accumulation. They further warned that such increased sedimentation rates should be considered when establishing mussel farms. Consequent to this, Mattsson and Lindén (1983) showed how a mussel farm in Sweden changed the structure of the underlying benthic fauna, much in the way expected (see above). Thereafter, results from different studies have been variable. Some studies have not detected any effects of biodeposition on the local environment (Crawford et al. 2003), whereas others have shown that bivalve farms may lead to organic enrichment (Navarro and Thompson 1997; Kaiser et al. 1998) and localized changes to benthic sediments (Chamberlain et al. 2001) and modification of the resident microbial (Mirto et al. 2000), meiofaunal (Mirto et al. 2000) and/or macrofaunal communities (Hartstein and Rowden 2004). Differences in the magnitude of a farm's influence likely depend on farm (e.g., farm size, stocking density and age of operation) and site (e.g., bathymetry and hydrodynamic regime) characteristics (Black 2001; Hartstein and Rowden 2004; Hartstein and Stevens 2005).

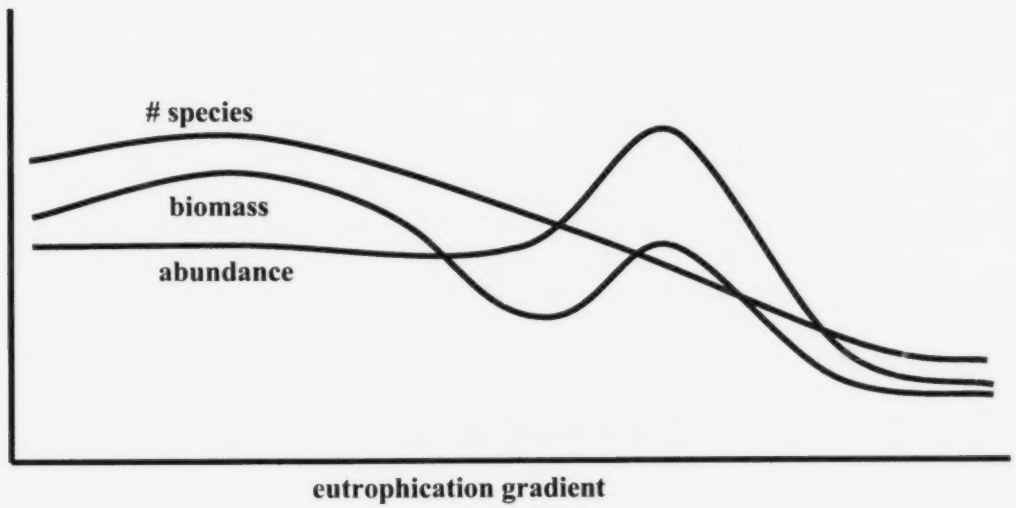

Figure 3. General model of soft-sediment benthic community response to disturbance (after Nilsson and Rosenberg 2000)

Shaw report. One study that is of importance to the Canadian situation is the "Shaw report" (Shaw 1998). This study examined the influence of mussel culture in Prince Edward Island in a series of 20 estuaries (= bays, 11 with and 9 without aquaculture). In each estuary, sediment cores were taken in each of 4 or 5 stations. In estuaries with mussel culture, stations were sampled both within and outside of the culture sites ("lease" and "reference" *locations*, respectively) and only from one *location* within estuaries with no mussel culture ("culture free") (in all cases, n = 1 sample location^{-1}). [Note that "lease", "reference", and "culture-free" locations are generally referred to as "impact", "control", and "reference" locations, respectively, in the monitoring literature (see Downes et al. 2002

for a full discussion of these terms) but here we will use the terms as described by Shaw (1998) to avoid undue confusion.] Cores were analyzed for water content, organic matter content, redox potential (Eh, at 6, 12, 18 and 24 cm depths), and sulphide concentration (at 4, 12, and 20 cm depths). A benthic enrichment index (BEI - Hargrave 1994) was calculated from these data. Benthic invertebrates were also sampled in one or two locations in each estuary (0.05 m^2 Eckman grab), from which a series of community indices were calculated. Flushing rates of the different estuaries were calculated and used as covariates. Each sample was also categorized as coming from "upper", "mid" or "lower" *position*, although this was not defined, and a given water *depth*, which ranged from 2 to 10 m. Two *age* (of culture) categories were also created (2-5 and 12-15 years). Samples were compared with respect to *position* and then by *location* separately for each *position*. Reference and lease *categories* were also compared separately for each *age* category. Different *depths* were also compared as were differences among *locations* for each *depth*. All the above analyses were done using ANOVA. Abundance/Biomass Comparison (ABC) curves (see Warwick 1986) were also calculated for each *location* and Bray-Curtis similarity measures between *locations* in each station were calculated. % OM data obtained in the study were compared to some historical data from 1971-72. Only the findings for each main factor (*location*, *position*, *depth*, and *age*) will be summarized here.

The various physical measures differed among treatments in different ways (see Table 1). With respect to physical measures, % OM, water content, and sulphides were typically greatest in lease samples and smallest in culture-free samples whereas Eh showed the opposite trend. Biological attributes did not always follow predicted trends (i.e., extreme values in lease and culture-free samples). The statistical significance of differences among *locations* differed considerably among indices. With respect to *position* within estuaries, only redox potential showed differences among *positions* (Eh was significantly greater in the upper position than the middle and lower positions in both the first and second sediment layers). With respect to culture *age*, % OM was greater in 2-5 year-old sites than in 12-15 year-old sites whereas this trend was reversed for Eh in the 3rd and 4th sediment layers. According to Shaw (1998), % OM, % water content and sulphide levels were all lower and Eh greater at depths from 2-4 m than at the other depths.

Despite the extensive nature of this work, its findings are, unfortunately, limited in their importance because the sampling design is poor and the types of statistical analyses done are either not clear in the report or simply incorrect. Pairing up *locations* within stations, although intuitively elegant, means that the samples are not independent. The degree of this non-independence is unknown and therefore there is no unambiguous statistical test that can be done (Underwood 1997). How flushing time was used as a covariate or how *position* was determined is unknown. Combining all the data from the different estuaries for each *location* to compute ABC curves simply does not make sense. Further, the differences in sample sizes between physical and biogeochemical (4-5 estuary^{-1}) and biological (1-2 estuary^{-1}) measures make comparisons about the utility of each of these impossible.

Table 1. Summary of results from Shaw (1998). Study examined various physical and biological attributes in 20 estuaries in Prince Edward Island in 1997. Observed values are shown from greatest to smallest (left to right) and groups underlined by a solid bar do not differ significantly.

Measure (layer)	greatest	intermediate	smallest
water content	lease	reference	culture-free
% OM	lease	reference	culture-free
sulphide (1)	lease	reference	culture-free
sulphide (2)	lease	reference	culture-free
sulphide (4)	lease	reference	culture-free
Eh (1)	culture-free	reference	lease
Eh (2)	culture-free	reference	lease
Eh (3)	culture-free	reference	lease
Eh (4)	culture-free	reference	lease
	culture-free	reference	lease
abundance	culture-free	reference	lease
biomass	lease	culture-free	reference
diversity (H')	reference	lease	culture-free
% deposit feeders	culture-free	reference	lease

The general conclusion of the study is that the small differences observed with respect to physical parameters have little influence on benthic communities. Given the uncertainties noted above with respect to the sampling design and statistical analyses, this claim is about the best that can be done. One interesting comparison that was done was that for % OM vs the historical data. This showed that % OM increased about 2-fold in each of the estuaries

compared (with and without mussel culture). This suggests two things. First, it will be hard to detect changes related to bivalve aquaculture in such a variable environment. Second, the importance of any such changes must be taken in context with respect to other factors that may be influencing the estuaries in PEI.

Macrofauna and associated taxa. As mentioned above, most work on the influence of suspended bivalve culture has largely concentrated on benthic processes (physical, chemical and biological) as they relate to increased organic loading associated with the practice (Carroll et al. 2003). With respect to the biological component, typically only infaunal communities are assessed. However, changes to the benthic sediment system may also have major direct and indirect effects on the more mobile and large benthic organisms. These organisms are not usually considered and yet are what people generally think of when they think of benthic biodiversity. Most work considers only near-field effects, ignoring far-field effects. When they are, typically only negative influences of aquaculture are considered (see, for example, Gibbs 2004). A more holistic vision of the role of bivalve culture in the ecosystem is clearly needed if management decisions about aquaculture sites are not to be made based on partial information (Davenport et al. 2003; McKindsey 2005). Bivalve culture has also been shown to have a number of "positive" effects on the ecosystem.

In its simplest form, bivalves and their associated fauna dropping off from suspended culture operations may enhance the amount of food available to benthic predators. The fall-off of mussels and other bivalves in suspended aquaculture may be considerable. For example, a daily average of 130 g m^{-2} of mussels (whole mussels only, does not include broken shells or empty shells in traps) fell daily to the bottom under mussel lines in the Magdalen Islands in the end of July, 2004 (Leonard 2004). There was also a marked increase in the abundance of large mobile predators (rock crab, lobster, and starfish) under the mussel lines at this time (McKindsey et al., unpublished data). A number of other authors have also reported a greater number and/or biomass of benthic predators that likely prey directly on bivalves from suspended culture within bivalve culture sites relative to control sites. These include starfish (Saranchova and Kulakovskii 1982) and crabs (Miron et al. 2002). Urchins are attracted to the fast growing kelp falling from mussel lines (MR Anderson pers. obs.) and benthivorous fish have also been documented feeding on mussels (Gerlotto et al. 2001). Gerlotto et al. (2001) measured an increase in fish density and production around mussel lines in the Mediterranean that they attribute directly to the increased prey availability at the farm site. Romero et al. (1982) studied the spatial distribution of crabs with respect to the location of mussel culture sites in one of the best studied systems with suspended bivalve culture, the Ría de Arosa in Spain. Over 4 seasons, they found that both the abundance and biomass of the 3 dominant crab species (accounting for 99% of the total crab abundance and biomass) was consistently (when significant) greatest within mussel farms, relative to control sites. In fact, there was on average more than twice the number of crabs within mussel sites than in control sites. In a subsequent study in the same area, Freire et al. (1990) showed that the diet of one crab species switches from algae being the most important component in a control site to mussels being the most important component in a mussel culture site. Similarly, Freire and González-Gurriarán (1995) studied the ecology of a second crab species and found that it too increased the proportion of mussels in its diet within mussel farms. This effect is not limited to crabs. Olaso Toca (1979; 1982) studied the distribution of echinoderms in the

same ría and observed 10 times the biomass of echinoderms (mostly starfish and sea cucumbers) within mussel sites relative to control locations, the starfish feeding on the mussels that had fallen from the rafts overhead and the seacucumbers feeding on settling particulate matter. Thus predators seem to make direct use of the mussels falling from culture sites. The abundance of sea urchins is also greater under these mussel rafts than in areas distant from them (Olaso Toca 1979, 1982). This has also been observed for oyster rafts in British Columbia (Brian Kingzett, pers. com.). Although this latter effect has not been quantified, it appears to result from urchins that have recruited to the raft falling off and accumulating in the immediate vicinity of the oyster rafts. In an ongoing study, D'Amours et al. (2005) found the abundance of several macroinvertebrate and fish species to be greater within a series of mussel culture sites than in control locations in Prince Edward Island. Inglis and Gust (2003) report that mussels on the bottom serve to aggregate the predatory starfish *Coscinasterias muricata* under mussel lines in Pelorus Sound, New Zealand, where they feed on fallen mussels. They suggest that this food source likely increases the starfish's reproductive output by enhancing growth and gonad maturation rates. Using modeling, they further suggested that this aggregating behaviour could also enhance fertilization success as it is a function of the distance between reproductive adults in broadcast spawners such as *C. muricata*. Taken together, it seems quite likely that the productivity of this species is clearly increased by the presence of bivalve aquaculture.

The physical structure provided by the mass of bivalves and associated fauna that fall from suspended bivalve operations also provides a habitat for species normally associated with hard-bottom communities. That is, suspended bivalve culture may change a softbottom benthic community into a hard-bottom benthic community (see Figure 2). For example, Kaspar et al. (1985) found that the build-up of live mussels and shell material under a mussel farm in New Zealand allowed for the development of a community with tunicates, calcareous polychaetes and sponges, species normally associated with hard-bottom reefs. In general, hard-bottom communities are generally more diverse, have a greater biomass (Ricciardi and Bourget 1999) and are more productive (Cusson and Bourget 2005b) than soft-bottom ones. Thus suspended bivalve culture may have indirect positive effects on local ecosystem diversity and productivity. Inglis and Gust (2003) found that living mussels and mussel shells covered 55% of the bottom within farm sites but were absent from non-farm sites, thus substantially increasing the physical structure within farm sites in New Zealand. Also in New Zealand, de Jong (1994) reports that the most noticeable visual impact of mussel farms is the reef-like structure that develops beneath them. In that study, clumps of mussels up to 20-30 cm thick covered 38 % of the seafloor beneath mussel line and reached a density of 250 m^{-2}. Although not quantified, Iglesias (1981) and Freire and González-Gurriarán (1995) also noted an abundance of mussels, shell and shell fragments in the Ría de Arosa and suggest that the additional physical structure in the system provides "habitat refuge" for associated species. Thus, that one species of crab they studied fed principally on another crab that lives associated with mussels is not surprising. Iglesias (1981) discusses the importance of this physical structure increasing habitat heterogeneity to augmenting the diversity of fishes under mussel rafts relative to control sites. They further mention how active predators are particularly abundant in this habitat, feeding on the associated organisms there. In fact, Iglesias (1981) typically found a greater number and biomass of fishes in mussel sites than in control sites and Chesney and Iglesias (1979) found the same trend for fish community richness, diversity and biomass although there

were temporal variations in these trends in both studies. Kaspar et al. (1985) similarly discuss the importance of how such a changed habitat is important for providing food to a variety of pelagic and epibenthic predators.

Associated organisms that are sloughed off also provide food to the benthos. For example, sloughing of kelp from mussel lines by storms or during harvest drops to the bottom under the lines and represents an attractive food source for bottom feeders such as urchins. Winter video surveys of the rocky bottoms under a mussel lease on the Northeast coast of Newfoundland show clusters of urchins feeding on healthy new growth of kelp under the lines. Crawford et al. (2003) reported similar clumps of filamentous algae fallen from mussel lines in Australia as the only visible effect of farms at these open coastal sites.

In sum, fall-off of bivalves and their associated organisms may transform soft-bottom benthic communities into hard-bottom benthic communities (see Figure 2), likely with much of the same ecology that regulates "normal" hard-bottom benthic communities. However, this assertion remains to be evaluated.

An increased biodeposition may increase the abundance of certain taxa of large epifauna. For example, Olaso (1979; 1982) reported a greater abundance of sea cucumbers in mussel culture sites than outside of them. Although many of these likely fell from the mussel lines overhead, Tenore and González (1976) also found that there was little unreworked mussel bideposits in the sediments underlying the mussel rafts; most had been reworked by the community there, including likely the sea cucumbers, the dominant species of which is a fairly non-selective filter-feeder (Costelloe and Keegan 1984). This also seems to be the case in British Columbia. Ongoing work by P. Barnes has shown that the abundance and growth of sea cucumbers there is also enhanced under oyster barges and may form the basis of interesting polyculture options.

Other types of indirect effects related to biodeposition are also possible. As discussed above and in a companion paper by Cranford et al. (in prep), the increase in organic loading associated with bivalve culture may greatly modify infaunal communities. Tenore and Dunstan (1973) studied biodeposition by three species of commercially important bivalves (the blue mussel, the American oyster, and hard clam) and found that elevated levels of biodeposition as is associated with aquaculture can enhance detrital food-chains, thereby augmenting the standing stock of benthic invertebrates and ultimately fisheries species. This may occur through a variety of indirect mechanisms. For example, several lines of evidence suggest that an increased abundance of several species at mussel aquaculture sites in the Magdalen Islands may lead to an increased productivity of these species through a complex cascading effect of aquaculture on the local environment. Winter flounder (*Pseudopleuronectes americanus*) is one of the dominant fish species in the lagoons of the Magdalen Islands and seems to have an increased abundance within mussel farms there. This species is particularly susceptible to predation by sand shrimp (*Crangon septemspinosa*), which are ubiquitous in most coastal areas in NE Canada, including the Magdalen Islands, and this susceptibility is size-dependent (Taylor 2003). Thus, the faster they grow and attain a size refuge from predation, the greater their contribution to overall productivity. Winter flounder shift their diet with ontogenetic stage, the smallest sizes depending mostly on small polychaetes (Stehlik and Meise 2000), which often dominate under mussel aquaculture sites because of increased nutrient loads (Mattsson and Lindén 1983). This switch towards a benthos dominated by small

polychaetes olso occurs in Grand Entrée lagoon in the Magdalen Islands (M. Callier, unpublished data). Unpublished observations that only the smallest size classes of winter flounder are more abundant under mussel lines support the model that mussel aquaculture increases the productivity of this species as only this sizeclass of fish may benefit from an increase in the abundance of small polychaetes. Similarly, Chesney and Iglesias (1979) report that an abundant goby in mussel culture sites eats a greater number of polychaetes when inside the sites than when outside of them.

Macrophytes. In Canada, the majority of resources for investigating environmental and ecological effects of aquaculture are dedicated to studies of finfish aquaculture. As such, it is surprising that finfish aquaculture-macrophyte community interactions in Canadian waters have received little attention (Hargrave 2003; Wildish et al. 2004a). That said, literature exists from studies of Mediterranean and Adriatic finfish culture. In these regions, seagrass beds (*Posidonia oceanica*) are naturally found up to depths of 40m due to high light penetration resulting from low turbidity (Holmer et al. 2003). Finfish aquaculture operations, however, have been linked to massive seagrass bed declines (Katavic and Antolic 1999; Ruiz et al. 2001; Cancemi et al. 2003). In the majority of areas where farms have been situated over seagrass meadows, the substrate has eventually become completely defoliated within the farm perimeter with effects still apparent within a 200-300m radius (Ruiz et al. 2001; Holmer et al. 2003). Initial hypotheses on the cause of these declines focused on shading effects of fish cages, however, no significant differences were found in light irradiance among farms and reference locations (Ruiz et al. 2001). Instead increased sedimentation, nutrient concentrations of phosphorous and nitrogen, and organic loading have since been linked to these effects and others (Ruiz et al. 2001; Cancemi et al. 2003). Further effects observed include: increased nitrophilic macroalgae coverage (such as invasive *Caulerpa racemosa*) along shorelines adjacent to farms (Argyrou et al. 1999) as well in defoliated patches in seagrass meadows (Katavic and Antolic 1999; Holmer et al. 2003), decreased growth of rhizomes, leaves, and shoots (Ruiz et al. 2001); decreased shoot density (Ruiz et al. 2001; Cancemi et al. 2003); increased concentrations of phosphorous and nitrogen in plant tissues (Ruiz et al. 2001); and increased epiphyte abundance leading to leaf fragility (Cancemi et al. 2003). Conversely, Ruiz et al. (2001) recorded decreased epiphyte abundances at farms but also increased abundances of the herbivorous sea urchin *Paracentrotus lividus* relative to reference stations and published literature from similar habitats. *P. lividus* feeds on seagrass leaf tips where greatest epiphyte concentrations are found and Ruiz et al. (2001) suggest these organisms were attracted to the vicinity of farms due to the increased palatability of seagrass tissues (from incorporating increased concentrations of fish farm-derived phosphorous and nitrogen). As such, these authors conclude low epiphyte abundances and subsequent declines in shoot density and cover may be the result of this increased herbivore pressure (Ruiz et al. 2001).

While mechanisms of interactions between natural aggregations of suspension-feeding bivalves and macrophyte communities have been clearly demonstrated, the same is not true for bivalves in suspension culture. That said, suspended bivalve culture could potentially result in negative as well as positive influences of on macrophyte assemblages via mechanisms related to their filtering capacity (decreasing turbidity and subsequently stimulating photosynthesis) and/or enhancing benthic-pelagic coupling (enhancing nutrient concentrations and cycling rates) through deposition of feces and pseudofeces (reviewed

by Newell 2004). The logical arguments put forth by these authors are generally derived from studies of natural bivalve assemblages, as previously described, or from anecdotal observations obtained during studies of benthic fauna. For instance, while examining benthic macrofaunal communities in and around Tasmanian bivalve farms, Crawford et al. (2003) observed abundant seagrass communities under oyster off-bottom leases in certain regions. Conversely, these authors also noted heavy macroalgal growth on suspended mussel longlines and subsequent sediment anoxia with patchy *Beggiatoa spp.* mats where these algae were believed to have fallen to the substrate.

In spite of the expansion of suspended bivalve culture internationally, increased recognition of the critical ecological roles of macrophyte communities, and observed global declines of seagrasses; no known published studies have addressed the issue of ecological interactions between this industry and macrophyte communities in a rigorous and scientifically defensible fashion. Such knowledge gaps must be filled if current DFO integrative management goals are to be achieved.

4.1c Bivalves in suspended culture (summary)

Bivalves in suspended culture may have a variety of influences on the ecosystem. Consider the very simplified food web of a coastal area is presented in Figure 2. Phytoplankton and fixed algae and plants are at the base of the food web that then supports zooplankton and larger invertebrates and fish in the water column and infauna (predators and deposit feeders) and filter-feeders and ultimately larger invertebrates and fishes on the bottom. There are also feedbacks with respect to nutrients that stimulate phytoplankton, algae, and plant growth. As discussed above, the presence of mussel lines, trays of oysters and other types of suspended culture has the analogy of adding what amounts to the addition of a hard-bottom benthic community into the water column, what we refer to as a "pelagic hard-bottom benthic community", or phb. The direct consequences of this include increased organic loading to the benthos and filtration of the phytoplankton and other things in the plankton. This increased organic load decreases the abundance of filter-feeders and large infaunal predators but increases the abundance of infaunal deposit-feeders and may also influence benthic algae and plants. There are also indirect, usually positive, effects on the abundance of large predatory organisms such as fishes and crabs. Depending on the rate of fall-off of bivalves from the suspended culture, there may also be the development of a "benthic hard-bottom community", or bhb. Both the pelagic (phb) and benthic (bhb) hard-bottom communities function more or less as do natural beds of bivalves in the manner in which it increases the abundance of associated species, including fishes and large invertebrates. Tenore and González (1976) show fairly convincingly that even if there is a loss of biomass directly under suspended bivalve culture (rafts) due to high rates of organic loading and subsequent changes to benthic biogeochemistry that the biomass of associated organisms on the mussels being cultured alone more than make up for any losses that may be brought about by organic loading. And there is also the increase in the abundance of macrofauna under the suspended culture.

It is interesting to note that all the typical infaunal responses to mussel culture (e.g., depauperate communities dominated by species typical of eutrophic environments) were also observed in the Ría de Arosa (Tenore and González 1976). However, when other components of the ecosystem were considered, the patterns discussed above were observed. In fact, we feel that it is important to note that the above review is an unbiased summary of

the available literature. When research has examined things other than benthic infaunal and geochemical responses, more "positive" effects of bivalve aquaculture are typically observed.

There are also a number of larger-scale effects that may occur. Pillay (2004) suggests that although there may be an area of reduced biomass directly below aquaculture sites, there will also be a transition zone some distance from aquaculture sites, in which enhanced organic enrichment will stimulate the growth of the benthos. A similar situation may be happening in one of the mussel farms in the Magdalen Islands where the biomass of infauna was greatest at intermediate distances from mussel culture sites (Figure 4). However, the other mussel farm in the Magdalen Islands did not show this trend and the communities did not differ markedly along transects there. Thus, the influence of bivalve culture is clearly very site-specific.

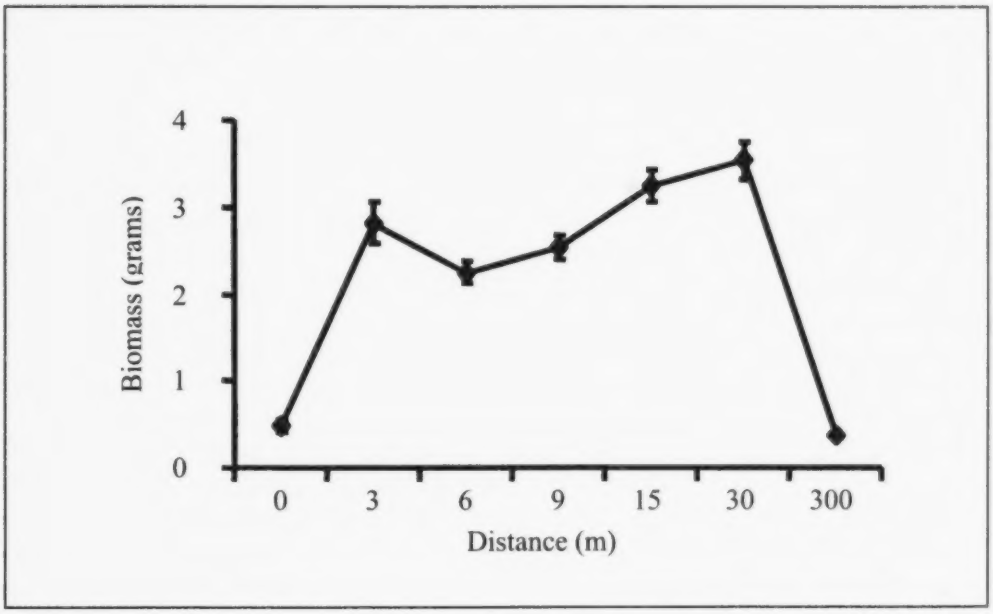

Figure 4. Mean biomass (± SE) of benthic infauna along transects starting directly beneath the last long-line in Grand-Entrée Lagoon, Magdalen Islands, Quebec (unpublished data from Myriam Callier).

In sum, the interactions between aquaculture and the environment are far from simple. Historical understanding of these interactions is limited to near-field effects and only a subset of these. Ongoing and future research will help address questions relating to ecosystem-level interactions. But these are doubtlessly very complicated and results are forthcoming.

4.2 Bivalves in bottom culture

4.2a Bivalves in bottom culture (water column effects)

Studies on environmental and ecological interactions of bottom culture of bivalves have focused, for the most part, on benthic effects. The majority of what is known about water column effects related to bivalve culture has been generated from studies of natural bivalve populations (mainly from the Chesapeake Bay region) as well as suspended aquaculture; which by its nature (typically much greater densities of bivalves), stands to have a greater influence on water column characteristics than bottom culture. As such, the remainder of this section will deal only with a limited selection of more recent literature on the ecological role of historic and current natural bivalve populations and the few existing studies on the influence of bottom cultured bivalves on water column variables.

American oysters were the dominant primary consumers in Chesapeake Bay that increased local habitat relief, heterogeneity and produced substrate for polychaetes, gastropods, barnacles, shrimp and crabs (Harding and Mann 2001). Many of these taxa that depended on the structure of oyster reefs were prey for upper level crustacean and fish predators. When numbers of oysters declined over the past century and most rapidly since 1970 due to overharvesting and destruction of oyster reefs and perhaps to a lesser extent also due to declining water quality and disease (Newell 1988; Rothschild et al. 1994), major changes were seen in the ecology of the bay. Newell (1988) calculated that there was a 100 fold increase in the time taken for oysters to filter the water of the bay (clearance rate) from 1870 to 1988 which resulted in increased phytoplankton densities, turbidity, and the other major predator of phytoplankton, zooplankton increased as did their predators the ctenophores and jellyfish. However, because zooplankton numbers are low in spring during phytoplankton blooms, much phytoplankton that would have been consumed by oysters now sank to the bottom producing anoxic conditions (Kemp and Boynton 1984; Newell 2004). Other estuaries along the eastern coast of North America have also experienced loss of oyster populations, and so probably also lost the benthic-pelagic coupling function that these populations once performed (Newell 2004). Newell et al. (2004) conducted a cost-benefit analysis which showed that oysters are of greater value to Chesapeake Bay for their impacts on improving water quality than as a fishery, and advocated enhancement programs to increase top-down control of phytoplankton.

Influences that suspension-feeding bivalves have on marine ecosystem processes have been extensively reviewed by Dame (1996) while Newell (2004) has reviewed information relating to the ability of bivalves to alter water quality in eutrophic temperate estuaries. These reviews focus on the filtering of suspended particles from the water column and deposition of faeces and pseudofaeces on the substrate. An adult oyster can efficiently filter particles greater than 3 µm from up to 34 litres of water per hour (Lavoie 1995) which in high densities of oysters (Kaiser et al. 1998) or mussels (e.g., Muschenheim 1992) can result in local depletion of phytoplankton and in some cases changes in plankton physiology, growth rates, and nutritional quality for predators (Prins et al. 1998). Unlike other suspension-feeding bivalves such as infaunal clams, American oysters and blue mussels maintain high clearance rates and do not reduce filtration rates when sestor levels increase. Instead, they reject phytoplankton that exceeds their needs along with less nutritious particles and silt as pseudofaeces. This process can reduce phytoplankton abundance, particulate organic carbon (Dame et al. 1984), and turbidity which in turn

increases light penetration and the depth to which benthic plants and macroalgae can grow. Phytoplankton populations may also be supported, however, by ammonia excreted by the bivalves and nutrients regenerated from faeces and pseudofaeces. In some cases, though, nutrient loads can actually be reduced from water bodies through bivalves changing nutrient regeneration processes in the sediment, as when nitrogen is permanently removed from sediments as N_2 gas (Dankers and Zuidema 1995) as well as through the removal of large amounts of nitrogen in cultured biomass (Rice 1999).

Bivalves may also alter the phytoplankton community through preferential removal of species larger than 3 μm diameter (reviewed by Newell 2004), resulting in dominance by picoplankton including cyanobacteria. Benthic bivalves may also influence phytoplankton through regulation of nutrients. Gibbs et al. (2005) estimated that beds of the horse mussel *Atrina zelandica* accounted for up to 80% of the nutrient supply for pelagic primary production in a New Zealand harbour. It has been hypothesized that release of inorganic nutrients into the water column by oysters may accelerate phytoplankton productivity (Leguerrier et al. 2004).

Bottom dwelling oysters may also have direct and indirect effects on zooplankton communities in estuaries and coastal areas. These effects may structure resident fauna both because zooplankton occupy intermediate tropic levels in estuarine food webs and because many estuarine zooplankton are larval forms of resident benthic and pelagic fauna. Harding (2001) reported that bottom-dwelling invertebrates (polychaetes, gastropods, barnacles, shrimps, crabs) associated with a restored American oyster reef influenced the composition and abundance of the overlying zooplankton community of bivalve veligers, gastropod veligers, polychaete larvae, barnacle nauplii, calanoid copepod adults and nauplii and decapod zoea. Reef-produced zooplankton are prey for planktivorous pelagic fish such as Atlantic menhaden (*Brevoortia tyrannus*) and Atlantic silversides (*Menidia menidia*) that are in turn consumed by striped bass (*Morone saxatilis*) and blue fish (*Pomatomus saltatrix*), and benthic fish and crabs. In addition, studies (reviewed by Newell 2004) have suggested that cultured bivalves may alter zooplankton communities by grazing on microzooplankton (40-300 μm diameter) and also by grazing of other suspension feeding invertebrates attached to aquaculture structures. Newell (2004) also suggests that high concentrations of bivalves might out-compete zooplankton, such as copepods, for phytoplankton at critical periods for zooplankton population growth.

4.2b Bivalves in bottom culture (benthic effects)

In addition to benthic interactions previously described for suspended bivalve aquaculture, bottom (and off-bottom) culture sites are further subjected to physical disruption of substrates, greatly influencing observed assemblage changes (Simenstad and Fresh 1995). The high prevalence of physical influence is mainly a function of this culture method generally occurring in intertidal or shallow subtidal zones (Boghen 2000b; Matthiessen 2001; Spencer 2002). Such physical disruptions may vary substantially in intensity and duration and are due to hydrodynamic alterations caused by tables, racks, or other culture infrastructure; substrate enhancement; lease maintenance and harvesting methods; and physical/chemical removal of predators. Considerable attention has been given to these areas in previous studies and in several comprehensive reviews (Simenstad and Fresh 1995; Deslous-Paoli et al. 1998; Kaiser et al. 1998; Jamieson et al. 2001; Kaiser 2001; Cranford

et al. 2003b; Newell 2004; Pillay 2004). As such, the following sections are meant to briefly summarize this material while updating recent findings not addressed by these authors.

Fauna. In general, bottom and off-bottom culture of bivalves occurs in soft-bottom systems such as lagoons and sheltered regions of coastal embayments and estuaries with relatively low current velocities. The addition of culture structures (e.g. lines, bags, racks, trestles, tables, predator exclusion netting) can further lower these current velocities. Measurements taken downstream of off-bottom oyster (*C. gigas*) trestles showed order of magnitude reductions in current velocity relative to upstream readings (Nugues et al. 1996). When these current reductions are combined with biodeposition from bivalve filter-feeding, increased sedimentation rates (both organic and inorganic) are generally observed (Ottman and Sornin 1985; Castel et al. 1989; Martin et al. 1991; Kirby 1994; Nugues et al. 1996; Forrest and Creese 2006; Mallet et al. in press). Forrest and Creese (2006) examined the benthic effects of intertidal *C. gigas* culture at a 24 ha. farm in New Zealand. Three-fold increases in sedimentation rate beneath racks in comparison to reference sites were observed (436 vs. 161-181 g $m^{-2}d^{-1}$, respectively) as well as up to five-fold reductions in sediment shear stress and increased organic matter concentrations below racks. Despite this, no sediment accretion was observed below racks due to enhanced erosion of these unconsolidated sediments (Forrest and Creese 2006). Similar observations of enhanced sediment erosion under off-bottom culture structures were found by Ottman and Sornin (1985) and Everett et al. (1995). Besides physical changes, Forrest and Creese (2006) described increased infaunal densities, particularly capitellid species, under racks. Multivariate analyses of density and composition data demonstrated clear farm-related impacts on macro-infaunal community structure, similar to the results of Nugues et al. (1996).

Spencer et al. (1996; 1997) also observed increased sedimentation rates in areas of Manila clam (*Tapes philippinarum*) bottom culture due to decreased current velocities. Comparison of reference sites and experimental clam plots with and without predator-exclusion netting demonstrated the presence of netting caused significant organic matter concentration increases along with a four-fold sedimentation rate enhancement. This situation served to elevate the substrate profile 10 cm, shift the infaunal community to dominance by deposit-feeding worms, and increase primary productivity (*Enteromorpha* spp.) which subsequently attracted *Littorina littorea* to these plots (Spencer et al. 1996, 1997). Related observations of increased primary productivity in the form of increased algal cover on predator-exclusion netting have been made by Simenstad et al. (1993) and Bendell-Young (unpublished data, cited in Jamieson et al. 2001). Ongoing research in Baynes Sound, British Columbia has also demonstrated that predator-exclusion netting of Manila clam farms increased siltation (Bendell-Young, unpublished data, cited in Jamieson et al. 2001).

Although these examples indicate generally expected results of investigations of bivalve aquaculture operations, other studies show the effects of sedimentation are variable and likely determined by site-specific conditions. For example, Crawford et al. (2003) found variation in sedimentation rates among various off-bottom oyster (*C. gigas*) culture sites to be much higher than variation among samples taken at culture and reference sites in the same system. Consequently, no significant differences were found in redox potential,

concentrations of sulfide or organic matter, or in macro-infaunal community structure (Crawford et al. 2003). As well, while Martin et al. (1991) reported sedimentation increases at off-bottom *C. gigas* leases, no difference between culture and reference sediments was detected two months after removal of the oysters, suggesting even when effects are found they may be relatively short-lived. More recently, in a 17-month study of an off-bottom *C. virginica* lease, Mallet et al. (in press) reported a 93% sedimentation rate increase relative to control sites. However, no significant difference in organic matter content, redox potential, or sulfide concentration of sediments were found when compared to reference sites. Conclusions regarding impacts to macro-infauna at the culture site were fairly ambiguous as a result of examining only annelid taxa. The absence of significant effects in this study was attributed to lower stocking densities relative to previous studies and the high frequency of sediment disturbance by wind-driven re-suspension and winter ice scour events in the study area. However, no data on the frequency, duration, or spatial extent of these disturbances are provided to support these suggestions (Mallet et al. in press).

Aside from altering current patterns, bottom and off-bottom aquaculture infrastructure has also been shown to alter benthic communities by acting as substrate for attachment for sessile epibionts as well as foraging and refuge areas for free-living fauna (Spencer 2002). Support for this is found in studies of fauna associated with *C. virginica* bottom culture in Rhode Island, USA. Dealteris et al. (2004) compared replicated samples from randomly selected submerged aquaculture gear (SAG; cages of oyster-containing mesh bags placed directly on the seafloor), submerged aquatic vegetation sites (SAV; samples from *Zostera* beds), and non-vegetated seabed (NVSB). SAGs displayed order of magnitude differences in abundances of fish, crustaceans, molluscs and also had larger abundances of sessile organisms such as sponges, hydroids, bryozoans, and ascidians relative to SAV and NVSB. Organism abundance was significantly correlated ($r = 0.94$) with the amount of emergent surface area available (Dealteris et al. 2004). While no significant differences in diversity were noted between SAGs and SAV, higher values were consistent at SAGs. Species unique to SAG included: American eel (*Anguilla rostrata*), oyster toadfish (*Opsansus tau*), rock gunnel (*Pholis gunnellus*), Atlantic tomcod (*Microgadus tomcod*) and American lobster (*H. americanus*). Other species observed were seaboard goby (*Gobiosoma ginsbugi*), grubby (*Myoxocephalus aenaeus*), tautog (*Tautoga onitis*), and cunner (*Tautogalabrus adspersus*). Northern pipefish (*Syngnathus fuscus*) and winter flounder (*P. americanus*) were unique to SAV sites while sand shrimp (*Crangon septemspinosa*) accounted for 87% of organisms sampled throughout the year at NVSB sites. As such, it was concluded that observed differences were due to differences in habitat composition, structure, and complexity which increased refuge areas, densities of fouling and forage organisms, thus demonstrating the ability of aquaculture infrastructure to act as vital habitat with the potential to increase secondary productivity (Dealteris et al. 2004).

Instances of physical disturbance due to equipment and personnel during maintenance and harvesting activities have been observed at off-bottom *C. gigas* culture in Ireland (De Grave et al. 1998). Heightened abundances of decapods reduced numbers of small crustaceans and fragile, shallow-burying bivalves in access lanes relative to control locations combined with no significant organic matter increases led the authors to conclude these results were caused by physical disturbance from vehicle and foot traffic. Similar disturbances of benthic fauna by hand and mechanical harvesting have been reported.

Species richness and density of three polychaete species were significantly reduced in areas where hoes were used for commercial digging for soft-shell clams in Maine (Brown and Wilson 1997). Westhead (2005) recorded similar findings where commercial harvesting of bloodworms (by hand raking) and soft-shell clams (by digging) in the Minas Basin resulted in immediate reductions in biomass and abundance of intertidal benthic macro- and meiofaunal communities. Further, community dominance shifted from sessile, tube-dwelling species (spioniod and maldanid polychaetes) to mobile opportunists such as harpacticoid copepods, nematodes, capitellids, and mud shrimp. No data were collected on post-disturbance recovery of biota, however (Westhead 2005). Dolmer et al. (2001) noted reduced densities of small polychaetes found after dredging for bottom cultures mussels while infaunal abundance and diversity decreased immediately following suction dredge harvesting of Manila clams from an area of muddy-sand bottom in Northern Europe (Spencer et al. 1998). That said, the infaunal community returned to reference conditions after only 1 year. In a related study, high mortality of non-target benthic fauna resulting from cockle (*Cerastostema edule*) harvesting by suction and tractor dredges was quickly and naturally alleviated with study sites becoming indistinguishable from controls within 56 days (Hall and Harding 1997). While significant effects are often observed immediately following bottom culture harvesting in unvegetated, soft-sediment habitat, quick recovery of invertebrate communities appears quite common (Kaiser et al. 1998).

Related disturbances such as modification of substrates by adding large volumes of gravel or crushed shells for cultch alter benthic communities to a higher degree. Gravelling mudflat and sandflat sites influenced epibenthic meiofaunal communities by increasing abundance and decreasing diversity relative to control plots at sandflats while mudflat species diversity increased (Simenstad et al. 1991). Despite being manipulated in the same manner, two differing responses were observed demonstrating the site-specificity of effects. Dominance shifts from deposit-feeding polychaetes to bivalve species have been noted in other studies on gravel enhancement (Thompson 1995). Despite the use of crushed shells as cultch material, no known published studies have examined the effects on benthic faunal communities, however, this method of substrate enhancement is expected to modify habitats and benthic communities in a manner similar to gravelling (Kaiser et al. 1998).

Concerted efforts are made in Pacific regions of the United States to control burrowing shrimp (*Neotrypaea* and *Upogebia*) which act to destabilize sediments and smother bivalve species through their burrowing action (Simenstad and Fresh 1995). In these areas, the insecticide carbaryl has been used historically (although its use is being phased out) despite literature demonstrating both lethal and sub-lethal effects on a suite of invertebrate and vertebrate species (reviewed by Simenstad and Fresh 1995). Neither this compound nor other chemical control measures are employed in Canadian bivalve aquaculture (Boghen 2000a; Jamieson et al. 2001); as such this topic will not be addressed further in this review. That being said, as culture operations expand into areas not traditionally considered suitable for bivalve bottom culture, scientists and managers should take note of the effects of these types of chemical control methods as growers may request their use (Jamieson et al. 2001). With respect to physical methods of controlling predators (hand-picking and/or trapping), no known published studies have assessed the responses of epibenthic communities to this practice.

While a multitude of studies document the varied responses, if any, of benthic communities to influences of bottom and off-bottom culture of bivalves, we are still in the introductory stages of understanding the whole picture. Specifically, most of these studies describe only alterations to benthic community structure, substantially fewer attempts to detail functional changes, even fewer still address modifications to primary productivity, and virtually no data exist on levels of secondary productivity in areas of bivalve aquaculture. Another shortcoming in our knowledge of this issue is a lack of experimentation which addresses the hypothesized mechanisms behind these observed community responses. Finally, if we are to effectively manage this industry in an integrative and holistic manner, studies examining ecosystem or "bay-wide" environmental interactions of bivalve aquaculture are necessary, as very few currently exist.

Macrophytes. While some physical effects of culture practices on macrophytes are indirect (altered nutrient cycling/pathways, increased turbidity or sedimentation) or unintentional (harvesting and personnel traffic), the majority of shellfish growers in some regions, such as the northwestern United States, have traditionally increased local water circulation for bivalve feeding by deliberately removing macrophytes from farm sites (Simenstad and Fresh 1995; Heffernan 1999). With the apparently high prevalence of this practice, it is surprising no studies could be found which have examined the ecological consequences of intentional macrophyte removals for aquacultural purposes. Related studies examining similar disturbances in a limited fashion are available, however. Peterson and Heck (2001) have experimentally demonstrated no significant difference in survival among mussels (*Modiolus americanus*) contained in seagrass (*Thalassia testudinum*) plots that had aboveground growth removed compared to un-manipulated seagrass plots. That being said, these plots measured $0.5m^2$ and are barely comparable to the magnitude of disturbance caused by clearing a culture site of many hectares. Further, no published studies could be found which have examined the impacts on changes to other taxa which also rely on seagrass habitat.

Everett et al. (1995) suggest density declines of *Z. marina* were the result of a combination of shading, sedimentation, erosion, and substrate disturbances during set-up and harvesting of oysters in stake and rack plots in the Pacific northwestern United States. Significant reductions in percent cover and shoot densities were found after one year of culture with almost no plants found after 17 months at rack culture sites. Similar reductions in eelgrass density and cover (upwards of 75%) have been recorded at stake and rack culture sites from this region (Carlton et al. 1991; Pregnall 1993).

Harvesting methods have also been found to heavily influence macrophyte communities in areas of bivalve culture. Peterson et al. (Peterson et al. 1987) compared various methods of clam harvesting (*Mercenaria mercenaria*). Harvesting with clam kicking boats caused a 65% reduction in seagrass biomass relative to controls and recovery was only partial after four years. Further, in areas harvested by hand-raking, which is perceived to have a relatively lower disturbance level, seagrass biomass decreased 25% (Peterson et al. 1987). Waddell (1964) noted oyster culture leases harvested by dredging displayed decreased shoot density, shoot length, and biomass compared to reference plots. Biomass was reduced 30% after one year and 96% after 4 years with effects persisting up to two years post-treatment (Waddell 1964). As such, it is clear that these harvesting practices cause substantial alterations to primary productivity in culture areas and these alterations can

persist many years after cessation of disturbance due to the time required for macrophytes (especially seagrasses) to recolonize disturbed areas.

In a comparison of current data and historical accounts, De Casabianca et al. (1997) suggest that macrophyte communities in the Thau Lagoon, France have shifted from a dominance of *Zostera* to communities composed of opportunistic algae (*Ulva* and *Gracilaria* spp.) over the past century. While a completely descriptive effort, these authors conclude this succession was caused by elevated levels of nitrogen and increased turbidity in these areas resulting from eutrophication by extensive off-bottom culture of oysters and mussels. In contrast, Deslous-Paoli et al. (1998) reviewed studies from the same lagoon (with no reference to De Casabianca et al. 1997) and compared historic and contemporary data on macrophyte distributions to conclude that *Zostera* spp. have extended their distributions from shallow regions to areas up to 5m depth in some areas of the lagoon. These authors attribute this increased distribution to reduced turbidity in culture regions as a result of bivalve filter feeding. On a near-field scale, macrophytes could be found between culture trestles but were completely absent underneath, indicating a shading effect of these structures (Deslous-Paoli et al. 1998).

Similar to studies of suspended bivalve culture, the majority of data available on interactions between bivalve aquaculture and macrophyte communities, with the exception of harvesting, are speculative at best. No published studies have tested these hypothesized mechanisms of influence through experimental manipulation of lease sizes, stocking densities, or duration of culture activities. Moreover, no studies have examined the impacts of bivalve aquaculture-related changes to macrophyte habitat on the population dynamics of species that utilize this habitat. This lack of study is especially interesting given the potential for positive effects of bivalve aquaculture on seagrass communities as suggested by Deslous-Paoli et al. (1998) and Newell (2004). Successful management strategies will require rigorous experimental testing of these hypotheses to determine precise causes of observed changes as well as accurately predict the magnitude and duration of these effects on macrophyte communities and their associated fauna.

4.2c Bivalves in bottom culture (summary)

In sum, there is yet no consensus in the scientific literature on whether dense bivalve populations contribute a net positive or net negative influence with respect to eutrophication of coastal ecosystems. Note that Newell (2004) makes no distinction between wild and cultured bivalves, or between suspended culture and bottom culture, in these potential mitigative effects on eutrophied waters except to say that at very high densities of bivalves, microbial degradation of very large quantities of biodeposits may deplete oxygen in the substrate resulting in release of P to the water column, buildup of hydrogen sulfide, and toxicity to benthic invertebrates. Because these bivalve densities are more likely to occur under cultured than wild conditions, environmental conditions should be carefully monitored at bivalve aquaculture sites. Although there are at times influence of bottom bivalve culture on benthic communities, these are often only short-term. Further, when there are effects, these may be seen as changes in infaunal communities (structure or altered abundances) or the associated macrofauna (fish and macroinvertebrates) such that their abundances are usually increased within culture areas.

4.3 Interactions between bivalve culture and birds and marine mammals

Birds and marine mammals are large charismatic species that live in areas where aquaculture of bivalves occurs and thus there is the potential for conflicts between these animals, bivalve farmers, and conservationists and the public in general (West et al. 2003; Hamouda et al. 2004; Roycroft et al. 2004). Although much is known about the interactions between bivalve culture and the environment, there is a paucity of published information with respect to the interactions between mussel culture and birds and marine mammals (Lloyd 2003). As mentioned above, bivalves form a source of food for not only humans but also for many other wild animals, including birds (Meire 1993). The importance of bivalves to the diets of many birds is underlined by the fact that many models have been developed to better understand the interactions between various bird communities (Goss-Custard and Willows 1996; Stillman et al. 2001; West et al. 2003; Caldow et al. 2004). Indeed, some nations evaluate the abundance of bivalves in an area to set catch rates that will not adversely effect local bird populations (Heffernan 1999; Smaal and Lucas 2000; Kamermans and Smaal 2002). Birds may also inflict serious losses on bivalve aquaculture leases, in both benthic and suspended culture and both at high and low tides. On the other hand, bivalve culture practices may also displace birds or else remove a part of the food source on which they depend, thus harming them (Kaiser et al. 1998). The importance of bivalve culture to marine mammals largely concerns entanglement, habitat disturbance/pre-emption, predation by otters, and faecal contamination of bivalve beds (Würsig and Gailey 2002). A full discussion of these interactions is given by Nash et al. (2000), Lloyd (2003) and Würsig and Gailey (2002) and will only be dealt with briefly here.

Positive effects. There are two major feeding modes for birds on bivalves: the waders (plovers, oyster catchers and the like) and divers (scaup, scoters, etc.). The first group of birds may profit from bivalves growing in beach culture whereas the second group may profit from bivalves being grown on the bottom at high tide and/or and in suspension. In its simplest form, the bivalves in culture provide food directly for many types of birds (Dankers and Zuidema 1995). In the case of suspension culture, Dunthorn (1971) and Davenport et al. (2003) suggest that mussels being grown have traits that make them particularly appealing to diving ducks, namely high meat content and thin shells. Indeed, Bustnes (1998) has shown that eiders discriminate and select mussels with these same characteristics. The change in habitat associated with bivalve culture may also result in a change in the associated community that may itself increase the abundance of food for certain birds. For example, Caldow et al. (2003) experimentally manipulated the density of mussels in an intertidal mudflat and monitored the abundance of birds in the area. None of the species monitored dropped in abundance and some increased, especially in areas where the availability of one of their preferred prey items, the amphipod *Corophium volutator*, was greatest. In an observational study, Roycroft et al. (2004) reported a greater number of species and abundance of birds in suspended mussel culture sites in Ireland than in a series of control sites. They suggest this was mainly due to the provision of perching areas (buoys, platforms, etc.) and to the diverse communities of organisms growing on the farm-associated gear offering an interesting food source for a variety of species. In fact, Boelens (cited in Roycroft et al. 2004) suggest that the general impact of suspended mussel production is generally positive for bird communities. Roycroft et al. (2004) also point out

that the common "impact" of increased number of crustaceans such as crabs and shrimps in mussel sites may also be a factor that could increase the abundance of seals in this habitat.

Negative effects. As with other groups of highly mobile predators, bivalve-feeding birds (and mammals) tend to aggregate where prey densities are greatest (Stillman et al. 2001). Thus birds may have a very serious effect on bivalve aquaculture operations. For example, Caldow et al. (2004) report that birds such as oyster catchers consumed 242 tonnes of mussels with a value of £133000 (19% of total landings) at Menai Strait, UK, in one winter. In the Dutch Wadden Sea, eiders and oyster catchers alone consume 21.8 million kg (fresh meat) of mussels and cockles yearly, much of it from cultured sites (see review in Dankers and Zuidema 1995). In Nova Scotia, a flock of scoters was reported to have taken 75% of the mussels in a mussel farm (Day 1995) and diving ducks may threaten the viability of some farm operations in Prince Edward Island (Thompson and Gillis 2001). Birds feeding on bivalves in culture may have population-level effects on the bivalves with consequent impacts on farming operations. Hilgerloh and Siemoneit (1999) modeled the impact of bird predation on a mussel bed in Germany and discovered that the preference of birds for large mussels would reduce the mean size of mussels in a site and thus increase the time to market. Diving ducks do considerable damage to mussels being grown in suspension in Europe and North America with common eiders (*Somateria mollissima*), scoters (*Melanitta* spp.), common goldeneye (*Bucephala clangula*), bufflehead (*Bucephala albeola*), and long-tailed ducks (*Clangula hyemalis*) being of particular concern in Canada (Ross and Furness 2000; Jamieson et al. 2001). For example, Galbraith (1987) estimated that eider ducks could each remove 2.6 kg of mussels each day in suspended mussel cultures, not including the portion that is simply knocked off during feeding. In Scotland, Ross and Furness (2000) show that 97% of the farmers there considered eiders to be a problem in their sites and that predation losses to the ducks amounted to between about 10 and 30 % through the mid 1990s. There is also usually a seasonal component to the impact of birds on bivalve communities. Seed and Suchanek (1992) suggest that damage to bivalve communities by birds might be greatest during the winter, when large flocks over-winter in coastal areas. Indeed, the fall migration period for ducks in Prince Edward Island also corresponds with the timing for mussel spat collection and socking, which is very vulnerable to predation because of its small size and preference by sea ducks (Dionne 2004; Dionne et al. submitted).

There are also possible human heath concerns with respect to the presence of birds in culture sites. Some of the most abundant birds that frequent bivalve farms are seabirds (mostly gulls) that scavenge in sewage outfalls, dumps, etc. These birds may thus act as vectors to transfer human diseases back to humans via the bivalves in culture (Davenport et al. 2003). Similarly, as many parasites of water birds complete their lifecycle by passing through a bivalve intermediate host, they may thus infect bivalves in culture, possibly reducing their fitness. Indeed, a recent study by Buck et al. (2005) suggests that mussels grown in suspension off-shore may become less infested by trematode parasites that are transmitted via a bird host.

Negative effects of marine mammals on bivalves are seen to be of less importance. With respect to marine mammals, although Würsig and Gailey (2002) suggest that the bivalve aquaculture industry suffers "significant losses" from river and sea otters, Nash (2000) suggest that the risk of large crop losses is small. Nash (2000) suggests that the greater risk

with marine mammals to bivalve culture is that of faecal contamination from growing populations of seals. Roycroft et al. (2004) found a trend of greater abundance of common seals in mussel farms than in control sites but this was not statistically significant. The authors point out that this relationship should be studied further and that seals do eat mussels in their normal diet.

A number of methods have been tested to reduce impacts from birds in bivalve culture. This includes modifying husbandry practices, something that may benefit both growers and birds (Caldow et al. 2004). Davenport et al. (2003) discuss how bird scaring measures such as gunfire are used to ward off birds from intertidal culture sites in northern Europe. Ross et al. (2001) showed that underwater recordings of chase boat engines played at regular intervals and reinforced by boat chasing were effective in reducing he abundance of eiders in culture sites. Nash et al. (2000) also suggest that acoustic deterrent devices may be the most effective method of deterring birds and marine mammals from bivalve culture sites but warn that most animals habituate to the noises fairly quickly. Dionne (2004) and Dionne et al. (submitted) recently evaluated a more passive method for suspended mussel operation in Prince Edward Island. They tested normal socking material with a biodegradable fraction with the idea that it would protect newly socked mussels from predation in the fall and spring but would degrade after that to let the mussels grow out normally. The results were promising although efficacy was a function of mussel size, indicating that a very close match between mussel and mesh size is necessary to ensure that mussels cannot migrate out of the socks and be eaten. A thorough review of the state of the knowledge for reducing impacts by diving ducks is given in Furness (2000), Ross and Furness (2000), and Dionne (submitted).

Aquaculture may also have negative effects on birds and marine mammals. One of the most direct impacts is harvesting of food resources on which animals depend. For example, Dankers and Zuidema (1995) suggest that historical over-fishing of mussel seed and market-sized mussels and cockles has had negative impacts on local bird populations in the Netherlands. Various modeling studies have also predicted that harvesting of bivalves may have a negative influence on bird populations (e.g. Goss-Custard and Willows 1996; Norris et al. 1998). There can also be indirect effects of harvesting on birds. For example, Kaiser et al. (2001) and Schmechel (2002) both discuss how decreased abundances of associated species following harvesting bottom cultures may have a negative influence on bird populations as some birds are more dependent on the associated species than on the bivalves themselves. Changes of the benthic communities associated with bivalve culture may also have a negative influence on bivalves and marine mammals. Würsig and Gailey (2002) discuss how changes to benthic infaunal communities associated with aquaculture may displace otters and near-bottom feeding porpoises and dolphins in suspended culture. Such an effect is also likely for sites where bivalves are seeded on the bottom and have subsequent impacts on the associated communities.

Closely related to this is the notion that bivalve culture may reduce habitat for certain species (Jamieson et al. 2001). Bivalve culture is often very extensive and thus vast areas may be involved. At times, the area is left more or less intact but at times parts of it may be covered with "car cover" or plastic netting for predator avoidance, increase spat-fall and reduce dispersion of seeded bivalves by currents (Simenstad and Fresh 1995). Thus a good proportion of certain locations may simply be unavailable to birds and marine mammals for

feeding. For example, Carswell et al. (in press) found that "car cover" may cover up to 22% of a particular habitat (substrate type and depth) for a given clam species in an area. In other cases, sediments may be modified by the addition of gravel or other measures, thereby altering the available habitat (Kaiser et al. 1998). Of course, these modifications may also have a positive influence on different bird species. Hilgerloh et al. (1999) studied the abundance and feeding activity of birds in and outside of an oyster culture (trestle) area in Ireland and found that although the number of species did not differ between the two areas, the abundance of several bird species was reduced within the culture site. The extensive nature of bivalve culture also means that marine mammals may be displaced by this activity. Markowitz et al. (2004) studied the spatial distribution of dusky dolphins in the Marlborough Sounds, New Zealand and found that they avoided the areas occupied by mussel culture long-lines. Numerous studies have shown that human disturbance may have an important influence on the distribution of shorebirds (Stillman and Goss-Custard 2002; Yasué 2005) and Kaiser et al. (1998) suggest that this may have an impact on birds in bivalve culture sites. As human disturbance also effects the distribution of marine mammals, activities associated with bivalve aquaculture may also influence this group of organisms (Lloyd 2003).

The physical structures associated with bivalve farms have been shown to have negative effects on birds and marine mammals. In an extreme example, Lloyd (2003) discusses how two Bryde's whales have been killed after becoming entangled in mussel spat collectors in New Zealand. This poses certain questions for the installation of offshore culture sites, especially where threatened species are concerned. They use the example of baleen whales, which cannot echolocate, and includes humpback and right whales. In the same paper, Lloyd (Lloyd 2003) discusses how the risk of entanglement is probably greatest for thin ropes or those that are not under tension. Large amounts of litter from bivalve culture may also be found on the seabed under mussel farms and on nearby shores (Cole 2002). Many marine mammals and birds may ingest or get tangled in such products and thus it may have a negative impact on them (Jamieson et al. 2001; Lloyd 2003). A particular example of impacts from bivalve culture comes from the west coast of North America where growers spray the insecticide carbaryl to kill burrowing shrimp in oyster grounds (Simenstad and Fresh 1995; Davenport et al. 2003). This practice has variable effects (Simenstad and Fresh 1995) with Dumbauld et al. (2001) suggesting that most are relatively short-term. However, changes to associated invertebrate communities do occur and thus may impact bird and marine mammal populations. In fact, Heffernan (1999) suggests that the method is more damaging than the current trestle method in Ireland and should not be used there.

There are also reasons to believe that greater scale trophic or food web interactions between bivalve culture and the general ecosystem may impact on birds and marine mammals (Lloyd 2003; Gibbs 2004). Such modeling usually emphasises the importance of zooplankton as the main mechanism to transfer energy up from phytoplankton to higher trophic levels, including fish, marine mammals and birds (Broekhuizen et al. 2002). In short, the conclusion is that a significant increase in the biomass of filter feeders in an area (the bivalves in culture) may largely replace the functional role typically filled by zooplankton and with consequent impacts on higher trophic levels (Gibbs 2004; Jiang and Gibbs 2005). However, as pointed out by numerous authors (e.g., Jamieson et al. 2001;

Broekhuizen et al. 2002; Butler 2003), these interactions are quite complex, have rarely been estimated, and remain largely theoretical.

5. MEASUREMENT OF FISH HABITAT EFFECTS

The evaluation of the contribution of different components to the functioning and productivity of the ecosystem is well beyond the scope of any type of monitoring programme. That being said, this goal should be the focus of concerted effort by scientists so that logical decisions about bivalve culture regulation may be made. As shown in a companion paper to this one (Chamberlain et al. 2006), great advances have been made with respect to PZDN (phytoplankton, zooplankton, nutrients, and detritus) models and these will not be expanded upon here. Such models are prohibitively expensive to develop and are more useful for planning than for monitoring.

The basic question is "what should be measured?" The type of benthic monitoring that is typically promoted includes remote methods for sampling benthic communities and sediment biogeochemistry. Although simple to measure, the use of biogeochemical measures are often fraught with user errors and their link to ecosystem productivity is largely unknown. Similarly, the link between benthic infauna and ecosystem productivity is equally ambiguous. What's more, biogeochemical methods are probably not relevant or simply not useable in situations where soft-sediments are not prevalent (e.g., beach culture or cobble bottoms) or when there is a heterogeneous bottom, as is often the case in deep-water sites in British Columbia. Other than the video methods that are discussed in Wildish et al. (2005) and Cranford et al. (in prep), the methods discussed therein do not address the issues developed in the current paper. That is, the larger organisms (fishes and macroinvertebrates) and the contribution they make to the productivity of the system are not considered, nor is the epifauna on the bivalves and culture gear itself.

As discussed earlier, larger taxa are usually more abundant in areas associated with bivalve culture sites (on and below culture operations) than outside of them. An overall change in productivity brought on by a bivalve culture site may not be negative as the productivity of the species that are associated with the bivalves in culture may compensate for any loss in productivity associated directly beneath the culture sites. What's more, the productivity of the benthic system may be enhanced at some intermediate distance from the farm, further enhancing the productivity of the system at some larger spatial scale. For these reasons, bivalve culture operations may have a net "positive" effect on the productivity of a system. Of course, there are very well-founded theoretical reasons and examples to imagine a scenario where organic loading as it relates to bivalve culture greatly exceeds the assimilative capacity of the benthic environment such that even mobile macroinvertebrates and fishes would no longer be present (Gray 1992). Clearly, in this scenario, larger taxa would not contribute to the productivity of the local benthic environment.

Without a solid understanding between these near-field and far-field effects, we suggest that at the very least the question "what should be measured?" should include an evaluation of these larger "important" (fishes and macroinvertebrates) species when considering the influence of bivalve culture on the ecosystem. We also suggest that the organisms associated with the bivalves in culture and the related equipment also be evaluated and considered. This may be done in a number of ways and are very well discussed in

Kingsford and Battershill (1998), Davies et al. (2001), Eleftheriou and McIntyre (2005b), and Wildish et al. (2005). Here, we only summarize some pertinent points.

Remote methods vs diving systems. There are many differences between using remote and diving systems. In the end, the choice of the method to be used will be a trade-off between the pros and cons offered by both techniques. One of the major differ differences is the precision between the two sampling methods. In simple towed or dropped systems, the video or still camera is, to a large extent, constrained to the area directly below or being the craft from which it is being operated. Further, because these apparatus inherently lack exactness in operation, many operators may prefer to steer wide of the lines or rafts and associated gear in order to avoid getting them entangled in the bivalve culture structure. Unfortunately, the influence of suspended bivalve culture is often localized to the area directly beneath the bivalves being cultured and thus observations directly beneath the (for example) mussel lines is important to evaluate their influence on macroinvertebrate and fish communities. Such localized effects are particularly difficult to sample (Wildish et al. 2005). Further, these remote methods cannot quantify the abundance of associated species on the bivalves in culture and the related equipment. Thus, for a more unbiased representation of these communities, sampling using scuba or other divers is likely important. However, diver-based systems are largely limited to more shallow waters and so cannot be used in deep-water systems to any extent unless mixed gasses are used and this turns a relatively simple task into a complicated one (see Munro 2005 for a general review of the use of diving systems for benthic surveys). In comparison, once remote methods are in place, they are typically much less complicated logistically (i.e., once in the field) and much more ground may be covered in a given period of time. Guided remote vehicles, while becoming more available, are not yet common and require a considerable capital investment and specialized operators.

Still and Video Photography. Wildish et al. (2005) and Smith and Rumohr (2005) provide excellent recent reviews of these methods, outlining the strengths and weaknesses of the different techniques, and we will not repeat the exercise here. In short, although still photographs typically give greater resolution that typical hi-8 video films, the recent availability reasonably priced of high-definition video systems should go some way to reduce this resolution advantage. Similarly, recent advances in ROV systems should reduce the problem of them not staying at a fixed distance from the bottom. Still and video photography also provide physical evidence of a situation and the data may be verified or "mined" in the future to evaluate other hypotheses.

Scuba diver counts. This approach is well described in Kingsford and Battershill (Kingsford and Battershill 1998) and Munro (2005b) and is the staple of much work done in marine ecology. It is also one of the most interesting approaches because it is fairly simple and all of the data are collected right away, without having to spend considerable time analyzing images in the office, and is thus fairly cost-effective. At the very most, audio recordings may be made and these transcribed rapidly following the dive. Further, as suggested above, divers may swim transects that pass directly underneath suspended bivalve structures to estimate the abundances of organisms there, thereby including all the areas within the farm. This is probably also the only way to obtain a realistic estimate of the abundance of organisms associated with the bivalves in culture themselves and the related equipment.

Traps. Trapping protocols are well developed for crabs and other macroinvertebrates as well as fishes, have been used by scientists for stock evaluations, etc, for a long time and are discussed in Eleftheriou and Holmes (2005a). There are a number of advantages of this approach. First, cages/traps may be deployed and retrieved from the surface, thereby simplifying data collection. Second, proper baiting or light traps may attract a variety of target species from a considerable distance. Third, traps may sample a number of organisms that are able to avoid trawls and other towed gear. Finally, they may also be used to sample in very heterogeneous environments. On the negative side, they are non-selective and some species and sizes or sexes of some species may avoid traps so they do not necessarily provide an accurate representation of the benthic communities.

Trawls, sledges, dredges, grabs, etc. There is a dazzling range in this class of sampling devices and, again, these are well described in Eleftheriou and Holmes (2005a). The main differences among the approaches is the difference between towed (trawls, sledges, dredges) and stationary (grabs) methods. With respect to the former, many trawls (e.g., otter trawls) are too large to be used to collect samples from beneath bivalve culture sites. In contrast, we (CW McKindsey et al.) have had considerable success using small beam trawls to sample between mussels lines separated by only 5 m (although a diver is needed from time to time to free up the trawl that becomes caught up in the lines occasionally). Unlike trawls that have their associated nets free behind them, benthic sledges have a heavy metal frame that encloses the net and are often designed to sample just above the bottom for epibenthos and may have doors to allow sampling to be done only once they reach the bottom. They are thus more appropriate for work in deeper waters. Dredges are designed to scrape off epifauna, etc, from hard surfaces or for limited penetration into soft sediments and collection of the organisms there. By themselves, grabs offer a bewildering variety of sampling devices. These are lowered from a stationary sampling platform and are mostly for less mobile benthos. Most are also only good in soft sediments. On the whole, grabs are not useful for evaluating macrobenthos.

Remote acoustic methods. With respect to aquaculture, acoustic methods have historically been used to evaluate the influence of this practice on the physical structure (topography and sediment type) of bottom sediments (Wildish et al. 1999; Gerlotto et al. 2001; Anderson et al. 2003; Wildish et al. 2004b). The methods generally seem to work quite well with Wildish et al. (2004b) reporting a good correlation between the observed backscatter and benthic infaunal communities. However, this does not include the suite of large organisms that we suggest being sampled. In contrast, recent work by Brehmer et al. (2003) has shown that these methods may be useful for evaluating the pelagic fishes associated with longline aquaculture sites. It is doubtful whether these methods would be useful for raft culture or benthic systems.

Bottom culture. Although many of the methods described above are useful and indeed appropriate for sampling clam or oyster leases at high tide, sampling of some parts of the communities may also be done at low tide using a number of methods. More appropriate methods here would include quadrat counts, fixed time counts, the use of drop nets and Carona buckets , etc., that are found in the intertidal marine ecology literature.

Sampling design. This section is perhaps the most important. Decisions about the types of methods to employ are moot if the sampling design is not sufficient to evaluate the hypothesis to be tested. Unfortunately, a just treatment of this issue is well beyond the

scope of this review. That being said, two recent reviews do a very good job of explaining the logical assumptions about survey designs (Downes et al. 2002; Munro 2005) without going into details about statistics, which are largely a distraction from designing an appropriate sampling programme.

In short, a sampling design must be sufficient to capture the spatial and temporal variations in the variables to be measured. To this end, sampling should be done at different periods of the year with different dates within each period. Simply sampling once in a season will not reveal seasonal effects as we have no idea of the normal temporal variation in the variation being measured. That is, differences among seasons may not be greater than differences within seasons; the analysis is confounded (Underwood 1991, 1992). Of course, we could say that we are not concerned about the conditions during the cold months as we expect *a priori* that any influence of bivalve culture will be greatest during the more biologically active and more hydrodynamically calm (i.e., less storms to stir up bottom sediments) summer period and limit sampling to then.

There are many approaches to addressing spatial variation issues. Here, we will not discuss the pros and cons relating to random, stratified, and systematic sampling regimes. Rather, we will discuss generalities as they relate to each of these approaches. At a small spatial scale, there must be sufficient replication of samples to describe well the variable being measured (e.g., Ferraro and Cole 2004 and references therein). This is also true at a larger scale, that is, within a bivalve culture site. Simply taking a series of measurements within a single location within bivalve culture site and then comparing it to another "control" or "reference" location is simply not appropriate as, as with temporal location discussed above, there is likely considerable variation among locations within a bivalve culture sit. The statistical and logical question to be asked is "is the difference we see between a culture site and control (or reference) site(s) greater than differences among locations within the culture site.

Monitoring strategies typically use one or the other of two approaches. A culture site is compared to one or more "control" locations or else the variable of interest is evaluated and compared along one or more transect(s) leading away from an aquaculture site. Both of these approaches are valid but the former approach may be more appropriate in more extensive bivalve culture operations. The latter may be more informative in point-source situations, such as raft cultures.

At the next larger scale, there is the debate between the BACI (Green 1979) and Beyond-BACI (or asymmetric) (Underwood 1991) approaches (although both of these also include a temporal component). In short, the former idea is based on comparing a putative "impact" site to a second site that is essentially the same in all ways except for the source of disturbance. In the latter approach, an "impact" site is compared to series of non-impact sites and the statistical and logical question asks if the differences observed between the "impact" site and the control sites is greater than the differences among control sites. Papers by supporters of both of these approaches may be found in Schmitt and Osenberg (1996) and are discussed at length in an unbiased way in Downes et al. (2002) and will not be discussed further here.

In sum, the sampling design used for a given monitoring program depends on the question being asked and the details of the particular site to be evaluated.

6. OTHER ISSUES (AIS AND STOCK TRANSFER)

There is much evidence that the transfer of bivalves for aquaculture purposes has been one of the major sources of introductions of exotic species (i.e., a species that has been introduced to an area outside of its natural range) throughout the world (Carlton 1992a, 1992b; Naylor et al. 2001; Streftaris et al. 2005). Indeed, some authors suggest that introductions of oysters have even been the major source of introduction of exotic molluscs (Carlton 1992a) and invertebrates in general (Wonham and Carlton 2005), historically contributing at least as many of the exotic species found in a given area as has international shipping. And this trend seems to continue today in Prince Edward Island at a regional scale with the spread of the suite of invasive tunicates that is plaguing the mussel industry.

There are two broad classes of introductions that may result from bivalve aquaculture operations. First, there are those exotic species that have been intentionally introduced into an area for aquaculture purposes. This includes most species being cultured on the west coast at the time (with the notable exception of the manila clam, which may have initially arrived with imported *C. gigas* stock!). Second, there is the suite of species that are associated with the introduced bivalves (Carlton 1989, 1999). These may include both "hitchhiking"(animals and plants that grow associated with the bivalves) species as well as diseases that may cause outbreaks in the same or other species (Barber 1996).

The role of these different classes of organisms on ecosystem functioning and the bivalve operations themselves and is well beyond the scope of the present work (see recent review in Landry et al. 2006) and will not be done here. However, the point should be made that the possible responses of ecosystems and bivalve culture operations to such introductions are extremely varied and range from benign, to "positive" to very "negative" and may occur at some distance form the site of introduction. Although some effects may be predicted a priori, some effects can never be predicted and may have catastrophic effects on some parts of the ecosystem (Branch and Steffani 2004).

The I&T procedures in place in Canada seem to work well enough when they are followed but these likely only slow down the spread of aquatic invasive species (AIS) that become established regionally and obviously cannot work if there is little enforcement. There appears to be considerable issues with respect to enforcement and participation of the growers on both coasts in Canada and thus spread of current AIS remains, to some degree, unchecked.

To date, research on AIS in aquaculture systems in Canada and elsewhere has largely been directed towards mitigation. Little effort has been invested towards understanding the role of this class of organisms on the functioning of the ecosystems. As a simple example, production carrying capacity studies do not (to our knowledge) include this as a source of competition to bivalves or as grazers on phyto- and other plankton although their potential impact is great. This shortcoming should be addressed so that the true risks associated with their presence may be understood and better managed.

7. SUMMARY AND KNOWLEDGE GAPS

Bivalve aquaculture has three main activities; 1) seeding, 2) grow-out and 3) harvesting. Most of the research and discussion relating to the interactions between bivalve culture and the ecosystem has focused on grow-out activities, with very little attention on the other two activities. However, unlike finfish aquaculture were the main alteration of the on the ecosystem is related to the addition of food, bivalve aquaculture is an extractive system, with the bivalves filtering out food from the water column. Although this does increase sedimentation rates locally, it also removes a large amount of nutrients at harvest time. Yet, the bulk of literature on the environmental impacts of bivalve culture focuses on the associated local increases in sedimentation. This provides a very truncated view of the role of bivalve culture in the ecosystem and other components must also be considered to ensure that managers have all the information to make appropriate decisions with respect to ecosystem-based management.

Changes in secondary productivity resulting from the installation of shellfish aquaculture structures have been observed or expected based on modifications of benthic (normal, bhb and phb, and intertidal) communities. To date however, development and application of appropriate monitoring techniques remain limited as is our ability to predict the direction or magnitude of the community response to shellfish farms. Here, we list a number of knowledge gaps that must be addressed in order to properly assess the true role of bivalve culture in the ecosystem.

1) The role (i.e., the sum of all the parts, including macroinvertebrates and fishes, the organisms associated with bivalves in culture, etc.) of bivalve culture in determining the productivity of the ecosystem;
2) The influence of harvesting on i) drop-off and consequent responses, ii) nutrient fluxes, iii) phytoplankton dynamics, iv) stability of the local ecosystem;
3) The influence of re-socking on i) biodeposit production, ii) nutrient fluxes, iii) epifaunal communities and consequent cascading effects;
4) The influence of bivalve culture on the planktonic communities;
5) Indirect effects on benthic and intertidal communities (via modifying recruitment);
6) Issues of scale and multiple sitings;
7) The influence of AIS in aquaculture and the ecosystem;
8) Relative importance of aquaculture in ecosystem.

8. CONCLUSIONS AND RECOMMENDATIONS FOR FUTURE RESEARCH

As discussed above, the majority of the research directed towards "ecosystem studies" of bivalve aquaculture has been directed at defining the "production carrying capacity" of a given water body. That being said, there are other definitions of carrying capacity, including the "ecological carrying capacity" of the system (*sensu* Inglis et al. 2000). Although the determination of the production carrying capacity of a system goes some way

towards defining the ecological carrying capacity, the two are by no means the same (see discussion in ICES 2005). The same is also true of the use of simple biogeochemical measures and infaunal communities. These address only a component of the ecosystem and cannot even be used in some situations (e.g. hard substrates) or may be of questionable value when working in protected coastal areas where organic loading is already very high.

As has been suggested for finfish operations (Wildish et al. 2005), the use of video and diver surveys can go some way towards addressing one of the important components of the ecosystem (i.e., macroinvertebrates and fishes) but one which is often not considered when management desires simple and strict guidelines. We feel that this is perhaps unwise as ecosystems are much more complicated than that and that a "negative" effect in one component may also result in a "positive" effect in another. With respect to bivalve culture operations, we believe that this is generally the case as we have come across no cases where net "negative" effects on macrofauna and fishes were observed. Some of these organisms are important commercial or recreational species are also the ones that most people think about when marine "biodiversity" is considered and thus there is a natural appeal to evaluating them.

That being said, with rare exception, we could not find studies that actually examined the role of aquaculture in the productivity of macroinvertebrates and fishes. We have outlined a series of logical reasons as to why this may be so but the support for these assumptions is simply lacking. A concerted effort should be directed at obtaining a better understanding of the role of bivalve culture on the productivity of these taxa.

Given the increasing importance of AIS in bivalve culture and in general, further research should be directed towards better understanding their role in the ecosystem. Research on mitigation, although useful for the industry and possibly the environment if the abundance of AIS be curbed, does not advance our knowledge of their role in the ecosystem as a whole.

To our knowledge, there are no comprehensive assessments of the potential role of bivalve culture on pelagic food-webs and their cascading effects on benthic and intertidal communities. There is much support in the scientific literature to suggest that such effects will exist but little research has been directed to this end. Again, an effort should be made to address this issue.

In sum, we suggest that a more "ecosystem-based management" approach be used when evaluating the influence of bivalve culture operations in the environment. Simple measures, as often currently used in monitoring environmental interactions of finfish farms, give a truncated view of the role of bivalve culture and cannot capture both the negative and positive effects of bivalve culture on the environment.

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